ECOLOGICAL CONSTRAINTS ON CHINSTRAP PENGUIN FORAGING BEHAVIOR: THE ROLE OF DIEL AND SEASONAL LIGHT CHANGES

by

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A THESIS

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The relationship between foraging performance and prey availability can only be accurately interpreted by understanding the environmental constraints on predator behavior. Penguins are considered visual predators, but little is known of how their foraging tactics are influenced by changes in light. Chinstrap Penguin foraging was examined during two breeding seasons to test the hypothesis that light is a constraining factor. Radio telemetry of penguin arrivals and departures revealed diurnal and overnight foraging. Overnight foraging was common during chick-brooding, but after chicks creched, penguins foraged mostly during the day suggesting a preference for diurnal feeding. Diet sampling indicated that birds were capturing mostly krill, but that fish were more common in overnight foragers. Penguins foraging by day were found to spend more time at sea during reduced light levels in one season, but not the other. This study shows that light plays a major role in determining the daily foraging of Chinstrap Penguins and the availability of its prey, but that its effects are often mediated by other constraints.

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CHAPTER I

INTRODUCTION

The life history of penguins is constrained by interactions between the species' biology and changing physical and biological factors of its environment. Fluctuations in the demography and breeding success of penguins are associated with large-scale changes in abiotic factors, such as the Southern Oscillation (Croxall 1992). In addition, the capacity of penguins to forage successfully and provision chicks is linked to the status of prey populations near breeding colonies (Croxall et al. 1988a, Trivelpiece et al. 1990). Studies attempting to relate foraging behavior to environmental factors, however, have typically integrated large portions of the breeding cycle and are therefore not sensitive to changes on shorter time scales (CCAMLR, 1988). Few studies have addressed changes in penguin foraging behavior that might occur within a breeding season (Lishman 1985a, Williams and Rothery 1990, Chappell et al. 1993a, Le Maho et al. 1993) and fewer have attempted to relate these changes to measures of the penguins' physical habitat (Wilson et al. 1993). Examining the nature of, and relationships between, physical and biological elements on short time scales may lead to a more accurate interpretation of larger scale processes. Daily and seasonal changes in light intensity, although likely to be important environmental determinants of foraging behavior in penguins (Wilson et al. 1989a), have received little attention.

In attempts to understand the relationship between foraging behavior and prey availability, the lack of information on at-sea foraging tactics has given rise to a necessary assumption that prey within a penguin's horizontal and vertical foraging range represents available food (Croxall et al. 1988b, Hunt et al. 1992, Croll et al. 1993). Knowledge of the physiological adaptations that facilitate foraging, such as diving capacity, has led to a better understanding of how penguins are able to narrow the spatial gap between themselves and their prey (Kooyman et al. 1982, Kooyman and Davis 1987, Kooyman et al. 1992, Chappell et al. 1993a, 1993b), thus limiting the scope of this assumption. Few studies have addressed whether constraints on senses, such as vision, might mediate the detection and capture of prey (Wilson et al. 1989a; 1993). It is commonly assumed, however, that penguins are primarily visual hunters even though absolute visual sensitivity and the importance of vision relative to other senses has not been established (Martin and Young 1984, Howland and Sivak 1984, Bowmaker and Martin 1985, Wilson et al. 1993).

Equally important in relating predator to prey is an understanding of the temporal constraints operating on one or both groups, especially if an objective is to know when predator and prey overlap. Penguins show physiological and behavioral rhythms related to light-dark cycles. For instance, rhythmic secretion of melatonin by the pineal gland in Adélie Penguins (Pygoscelis adeliae) is linked to an endogenous clock; a clock that has a 24 hour cycle when birds are exposed to constant darkness, a 12 hour cycle in birds exposed to a 12 hour light: 12 hour dark regime, and is suppressed in birds experiencing continuous daylight (Cockrem 1990). Body temperature, thought to be mediated by melatonin, follows the same pattern. Adélie Penguin behaviors within the colony, such as

restlessness during incubation and ecstatic displays, also appear to have endogenous rhythms related to the diel light cycle (Müller-Schwarze 1968, Derksen 1977).

Daily cycles in light intensity thus have potential to constrain the physiology of a penguin in two ways: 1) by altering a bird's ability to use vision in perceiving its surroundings, and 2) by entraining a bird's activity pattern through hormonal control. Given these mechanisms it is not surprising that foraging activity has been linked to diel periodicity of light levels (Wilson et al. 1989a, Wilson et al. 1989b, Golombek et al. 1991), even at latitudes where colonies are exposed to continuous daylight during the austral summer: Yeates (1971) reported that at Cape Ross (77°S) in January Adélie Penguins tend to be away from the colony during the middle of the day. Williams and Rothery (1990) showed that during chick-brooding 96% of Gentoo Penguins (Pygoscelis papua) at Bird Island (54°S) forage exclusively by day. Other studies on Gentoo and Chinstrap Penguins (Pygoscelis antarctica) at King George Island (62°S), Jackass Penguins (Spheniscus demersus) at Saldanha Bay, South Africa (33°S), and Magellanic Penguins (S. magellanicus) in Argentina (42°S) revealed a similar predominance of diurnal foraging (Trivelpiece et al. 1986, Wilson 1985, Scolaro and Suburo 1994).

Further studies on Adélie, Chinstrap, and Gentoo Penguins show that birds taking overnight foraging trips spend less time swimming per unit time at sea than those taking diurnal trips thus concluding that penguins do not forage as actively at night (Adams and Wilson 1987, Wilson et al. 1989b). However, Macaroni (Eudyptes chrysolophus) and King Penguins (Aptenodytes patagonicus) at South Georgia (54°S) expend considerable diving effort at night (Croxall et al. 1988b, Kooyman et al. 1992), although more recent

studies on a number of species of penguins suggest that nocturnal foraging is characterized by lower capture rates (Wilson et al. 1993, Pütz and Bost 1994). Even though both latitude and season affect daylength and light intensity, making inter-site comparisons more difficult to interpret, it still appears that feeding at night is not commonly employed and that under lower light conditions birds are less successful at capturing prey.

While revealing much about penguin foraging and how patterns differ with time of day, the above studies have not examined how patterns change under different light conditions experienced during foraging. This information would provide a more controlled test of the importance of visual orientation during foraging. In addition, all but one previous study (on Gentoo Penguins; Williams and Rothery 1990) lack information about the foraging routine of individual penguins relative to the diel light cycle throughout the chick-provisioning period. Understanding how changes in ambient light intensity regulate a penguin's ability to obtain food is crucial, however, to interpret accurately the relationships between predator performance and prey availability.

This study used radio telemetry and food sampling to examine the foraging (i.e., activity patterns, trip frequency, time spent at sea, diet composition and mass) of Chinstrap Penguins, during two breeding seasons, relative to the light-dark cycle and daily light levels. The primary objectives were to: 1) describe Chinstrap foraging patterns and, more specifically, determine the relative importance of nocturnal foraging; 2) test whether reduced light constrains foraging behavior; 3) test whether seasonal changes in light or breeding behavior influence foraging; 4) relate the timing of foraging to the composition and mass of food brought ashore by penguins to determine how changes in diet might also

reflect adaptations to a dynamic light regime; and 5) examine whether these aspects of their foraging reflect unique conditions characteristic of a particular season or are persistent between years. Pursuing these objectives at Seal Island, Antarctica provided the opportunity to study a species that is known to forage periodically at night (Bengtson et al. 1993) and that experiences considerable diel periodicity in light during the breeding season (i.e., about 8 $\log_{10}$lux).

CHAPTER II

MATERIALS AND METHODS

Species Description

Chinstrap Penguins (4 kg, 71-76 cm) are the smallest of the medium-sized brush-tailed penguins (Genus: Pygoscelis; Clark 1906, Croxall and Furse 1980). During the breeding season, they feed primarily in inshore waters near breeding grounds (White and Conroy 1975, Croxall and Furse 1980) by pursuit-diving to depths typically less than 40 meters and rarely greater than 100 meters (Lishman and Croxall 1983, Bengtson et al. 1993). Most of the world's population (> 90%) breed on ice-free land along the Antarctic Peninsula and the islands of the Scotia Sea. The population of Chinstrap Penguins within the South Shetland Islands is estimated at 1.6 million individuals, composing more than 90% of penguins breeding there (Shuford and Spear 1988). At Seal Island, an estimated 40000 adult Chinstraps arrive each year in early November to establish nests. Upon hatching one or two chicks in late December, parents begin making daily foraging trips while alternating brooding duties with their mates at the nest. During mid-January chicks are left unattended for the first time (creche phase), and adults, continuing daily feedings, appear to forage independently of one another until chicks fledge at 55-60 days (Lishman 1985a).

Description of Study Site

Fieldwork was conducted at Seal Island, South Shetland Islands, Antarctica (60°59'S, 55°23'W; Figure 1), one of many small rocky outcrops in an island archipelago approximately 10 km north of Elephant Island. This study was carried out during the austral summers of 1993 and 1994 at two penguin breeding colonies: North Cove, a colony of approximately 900 nests located on the landward side of a large intertidal pool about 70m from the open sea, and Colony 72, with approximately 400 nests located on a 300m long beach overlooking Beaker Bay (Figure 1, inset).

Measurement of Foraging Patterns

The presence or absence of penguins at their breeding colony was recorded using radio telemetry on adult Chinstrap Penguins provisioning chicks from 9 January to 14 February in 1993 and from 8 January to 10 February in 1994. Radio transmitters (Advanced Telemetry Systems, model 2) were deployed on one adult from each of 80 nests (1993, n = 40; 1994, n = 40) haphazardly selected at North Cove colony. To minimize disturbance, birds were opportunistically captured, after having been relieved by arriving mates. Nest sites were marked with stakes and numbered on a photograph of the study plot to facilitate subsequent observations. A transmitter was attached to the middle of the penguin's back by securing a layer of outer feathers to the underside of the instrument using a plastic cable tie. A small amount of five-minute epoxy (< 5 g) was applied between the layer of feathers attached to the instrument, and the layer beneath it,

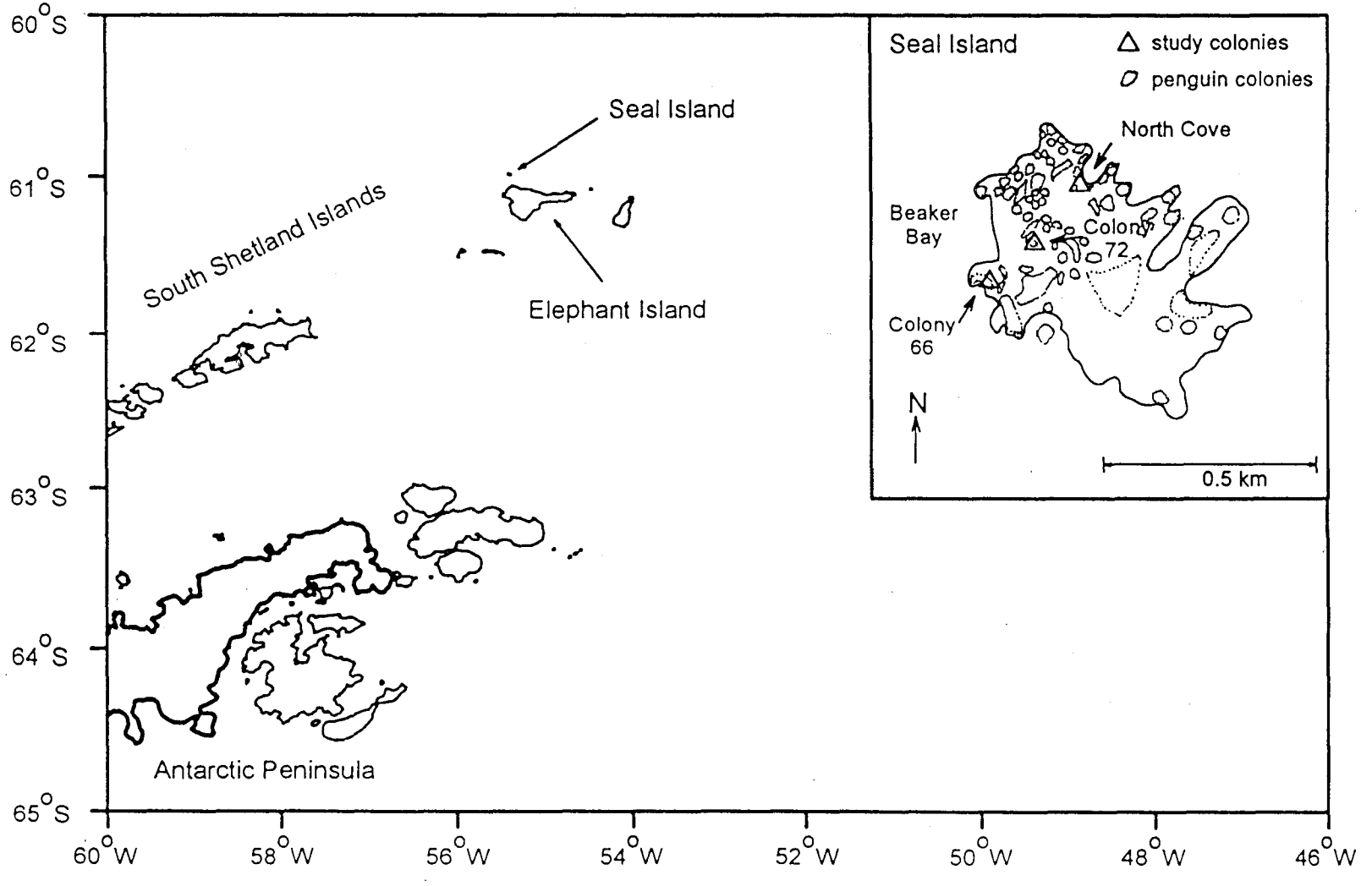

Figure 1. Location of Seal Island within the Antarctic Peninsula region and the relative positions of study colonies on Seal Island (inset)

to prevent the instrument from pivoting away from the body thereby damaging the feathers or allowing seawater to penetrate. A thin layer of epoxy was also applied to the underside of the instrument and around the cable tie to further insure that the instrument would not fall off prematurely. The instruments were left to fall off during the penguins' annual molt. The transmitters were positioned as far back on the bird as possible to minimize flow disturbances (Bannasch et al. 1994) but not so far back as to make the instrument more conspicuous by having the antenna (29 cm in length) extend beyond the tail feathers. The instruments were wedge-shaped at the anterior end, had a frontal cross-sectional area of 1.4 cm^2, weighed 20 g, and were usually positioned posterior to the point of the bird's maximum girth with the antenna lying flat against the animal's back behind the instrument. One device in 1994 stopped transmitting during the bird's first trip to sea and was removed during the subsequent visit.

Transmitters were deployed on adults provisioning chicks that were 1 to 2 weeks old (1993, 7-8 January; 1994, 6-7 January). The foraging activity of instrumented penguins was measured beginning one day after all 40 penguins were fitted with transmitters in an effort to reduce the effects that handling the birds and disturbing the colony may have had on foraging behavior. Foraging records were collected for 37 and 34 days in 1993 and 1994, respectively, with the end date in both years determined by the beginning of fledging (1993, 14 February; 1994, 10 February). The timing of departures from and arrivals to the island was registered by an automated receiving system that recorded the presence or absence of each radio-tagged bird during a ten second interval every fifteen minutes. Because radio tag signals are quenched in seawater and penguins

enter or leave the water at North Cove, it was possible to determine accurately the 15-minute interval during which foraging trips were initiated and terminated. Departure and arrival times were used to determine foraging trip durations which are defined as the actual time spent in the water potentially foraging. All arrival and departure times were converted into local apparent time (i.e., 1200 h occurs when solar angle = 90°) for Seal Island to facilitate comparisons with other study sites. By convention, the date on which birds departed was used in the analysis of activity patterns and other mean parameters that were calculated on a daily basis.

Visual observations confirmed the status of offspring at each study nest throughout the chick-brooding phase until creching began. In both years all nests had at least one chick until the beginning of creche (1993, 23 January; 1994, 20 January). After chicks creched (i.e., were left unattended), observations of chick-parent interactions were less frequent because adults spent progressively less time in the colony (Lishman 1985a). Nest observations were not continuous, usually lasting 2 to 5 hours each day, thus dates on which both adults were absent from the nest are estimates of the actual timing of creching. Chicks that have creched are intermittently guarded by parents, usually in the early morning and evening (personal observation). Thus, the timing of observations can affect when creching is detected. Some chicks probably creched before it was recorded, but because observations were typically conducted midday, when a minimum number of adults were present, this bias toward slightly later creching dates is believed to be small.

Criteria to Exclude Non-Provisioning Foragers

Because the status of nests could not be confirmed as frequently during creche, I developed criteria to exclude foraging records from adults that may have stopped feeding chicks sometime after creching. Using data only from birds that were provisioning chicks ensured that the measures of foraging behavior included in each year's sample were not affected by failed breeders which were not subject to the same foraging constraints.

Penguin nest failures during creche phase most often occur as the result of predation or starvation (Emslie et al. 1995; Davis and Miller 1990). Brown Skuas (Catharacta lonnbergi) have been observed at North Cove to feed on eggs and smaller chicks, although their success as predators seems to diminish later in the season when chicks are larger (Davis and McCaffrey 1986; personal observation). Giant petrels (Macronectes giganteus), however, are more frequently seen later in the season capturing chicks at the periphery of several colonies at Seal Island (personal observation) and at other breeding sites in the South Shetland Islands (Emslie et al. 1995). North Cove appears to be an exception; Giant Petrels are not common here during the breeding season probably because steep inclines near the inland edge of the colony and a fur seal rookery bordering the seaward edge block access to the periphery of the colony.

Starvation, as the result of desertion, was therefore assumed to be the most likely source of mortality among chicks at North Cove. Cases when adults would stop visiting the colony, presumably abandoning their chick(s), were detectable in the foraging activity records providing a basis to exclude data from birds that were less likely to be

provisioning chicks. If a penguin did not come ashore on a particular day during the observation period, subsequent foraging trips were excluded from analyses. Those birds which did visit the colony every day were assumed to have continued feeding chick(s) throughout the creche phase. While some birds might have visited the colony daily without feeding chick(s), this behavior seems unlikely given the energetic cost of traveling to and from the colony each day without an obvious benefit to reproductive output.

Determination of Fledging

Determining the endpoint of the study by observing fledging at North Cove was not possible because the chick(s) of study birds were not uniquely identified and the colony was too large to conduct accurate chick counts. Alternatively, an index of fledging chronology was based on daily counts of the number of chicks at a smaller, more isolated colony of approximately 300 nests (Colony 66; Figure 1, inset) during the period after creching had begun. The beginning of fledging was estimated as the date on which the mean of three replicate counts dropped at least 5% between successive days.

No studies have specifically addressed the foraging behavior of penguins once they stop feeding chicks prior to fledging. Whether parents continue to make regular trips to sea or change their foraging strategy as they prepare to fast during their annual molt is unknown. Using an estimate of the beginning of fledging as an end date for the study limited the inclusion of foraging records from birds that stopped feeding chicks thus potentially altering their foraging behavior. Growth studies on Chinstrap chicks at Seal Island (unpublished data) and Deception Island (Moreno et al. 1994), however, suggest

that parents stop feeding chicks when they are 43-50 days old (i.e., chick mass asymptote), a period as much as a week prior to fledging at Seal Island. Thus, it is still possible that study birds either reduced or terminated the feeding of chicks during the creche period.

Food Load Sizes and Diet Composition

Diet composition and mass of food brought ashore were determined by extracting stomach contents from penguins at Colony 72 using a lavage technique (Wilson 1984). Birds that had just completed a foraging trip were captured after they reunited with their mates at the nest but prior to feeding their chicks. Birds were held in a vertical, head up, position while 300 ml of tepid water was pumped into their stomachs via a veterinary catheter. The bird was then tipped approximately 30° below horizontal so that its culmen was pointed downward. Slight pressure was then applied to its abdomen after which the bird would typically begin regurgitating its stomach contents into the sample bucket. In 1993, each bird's sample was collected in a single bucket, whereas in 1994, the digested portion (i.e., individual prey in pieces) was collected in a separate bucket from the mostly intact portion of the sample, which was always egested first. During 1993, birds were lavaged until either 1) only clear water was recovered, or 2) they showed signs of distress (i.e., absence of aggression, inability to stand unassisted, or labored breathing), or 3) after the fourth lavage was completed, which was deemed the most disturbance allowable. In 1994, the methods were refined by eliminating the option of stopping when it appeared their stomachs were empty. It was discovered that while occasionally no obvious material

would be extracted during the third lavage, food would sometimes reappear during a fourth lavage. While this procedure meant that some birds were lavaged after their stomachs were empty, it provided greater uniformity in the extent of lavaging and reduced bias due to undetectable hard parts that could be present at the bottom of the stomach. Considering the change in procedure between years, caution should be exercised when comparing results between years. Five birds in 1993, all arriving in the evening, appeared to have empty stomachs and were lavaged only three times. One bird in 1994 showed signs of distress and was released after the third lavage.

Food samples were collected from five different birds every five-day period throughout chick provisioning (1993, 6 January - 3 February, n = 35; 1994, 8 January - 12 February, n = 40). Sampling was conducted on birds arriving in the morning (0700-0900 h; 1993, n = 15; 1994, n = 20) and in the evening (1700-1900 h; 1993, n = 20; 1994, n = 20), alternating between five-day periods.

Samples were drained, weighed, and sorted into primary prey categories (i.e., krill, fish, squid) and then reweighed to determine percent composition. The mass of each sample determined in 1993 represents the weight after the initial straining of the whole sample. In 1994, the total mass of each sample was recorded as the sum of the mass of each prey component rather than a pre-sort weight as in 1993. During the sorting procedure more water drained out of the sample prior to weighing the prey categories. Thus, samples in 1994 could be biased toward a slightly lighter masses compared to 1993.

Soft parts, consisting primarily of krill and fish, were preserved in a 10% formalin solution and stored for future analyses. Hard parts, consisting of fish otoliths and squid

beaks, were stored separately in isopropyl alcohol and later enumerated and identified to species. In this study, I will present results concerning the total mass and gross composition of the samples in addition to more detailed analyses relating to the fish prey.

Estimates of Light Intensity during Foraging

The average light intensity experienced by foraging penguins was estimated by measuring the relative ambient illumination at the top of the island (approximately 120 meters above sea level) using time-depth recorders that were equipped with light sensors (Wildlife Computers, Redmond, WA., USA). While the light conditions measured at Seal Island are not precisely what the penguins would experience on their foraging grounds (3-26 km offshore; Bengtson et al. 1993) it is believed to be a reasonable approximation. Relative illumination measurements were recorded every 30 seconds during periods that coincided with the radiotelemetry study at North Cove (1993, 18 January - 4 February; 1994, 9 January - 3 March). The overall amplitude of relative illumination measurements was adjusted to correspond with a theoretical range, as determined by known illuminations given solar elevation for the same dates (U.S. Navy 1952), by first arriving at a conversion factor C according to the equation:

$$\frac{Max^{R} - Min^{R}}{Max^{T} - Min^{T}} = C \text{ (Relative light units} \cdot \text{lux}^{-1})$$

where Max^R = the maximum relative light measurement taken during the day (1993, 1 February; 1994, 13 January) during the period corresponding to the telemetry study, Min^R = the minimum relative light measurement taken at night (1993, 30 January; 1994, 13

February) during the same period, Max^T = the maximum theoretical light (assuming no cloud cover) that would occur at solar noon on the same day that Max^R occurred, and Min^T = minimum theoretical light that occurred at solar midnight on the same date as Min^R. All relative light data were divided by the C calculated for each year to arrive at corrected lux measurements. This transformation equalized the daily amplitude of the relative and theoretical lux data. The elevation (i.e., relative magnitude) of the two scales was equalized by subtracting the absolute difference between Max^R and Max^T from all corrected lux measurements thus arriving at values termed approximate lux measurements. This approximation of the actual lux values does not take into account the sensitivity threshold of the light sensors at lower light levels (i.e., below one lux). While this would tend to artificially elevate night-time light measurements, the effect would be negligible considering that the difference between the approximate and theoretical illumination for a given sample taken at night would be less than one lux. In addition, as light measurements are averaged over the length of penguins' foraging trips, during which light can vary by up to 8 orders of magnitude, these differences become virtually undetectable.

Values of theoretical natural illumination available by time of day were determined by calculating solar elevation according the equation (Wilson 1989a):

$$\sin \gamma = \sin \phi \cdot \sin \delta + \cos \phi \cdot \cos \delta \cdot \cos t$$

where γ = solar elevation (°) at given times of day, ϕ = geographical latitude (°), δ = solar declination (°) for a given date, and t = solar angle by time of day (°) (e.g., 0° = noon and 180° = midnight). Solar declination values were determined using the

Nautical Almanac (U.S. Navy 1993; 1994).

Light measurements taken every 30 seconds were averaged into 5-minute means prior to subsequent analyses. Average light levels experienced during foraging trips were calculated as the mean of five-minute means that occurred during the time the penguin was at sea. Daily means of five-minute mean light measurements were calculated (midnight to midnight) and subtracted from the daily mean of the theoretical light values for each day to provide an index of how light conditions on a specific day compare to the expected conditions given a cloudless day. This was termed the brightness index and was used as a relative comparison measure of light conditions between days. A comparison of overall light conditions between years was not possible due to differences in the sensitivities of the light sensors used each year. However, periodic notes taken on degree of cloud cover did not suggest a substantial difference in light availability between years.

CHAPTER III

RESULTS

Characteristics of Foraging Trips

During the study in 1993 and 1994, the frequency distributions of arrival and departure times of radio-tagged Chinstrap Penguins were bimodal (Figure 2). Upon closer inspection of individual foraging records it became apparent that the periodic nature of the arrivals and departures indicated two general types of foraging: 1) diurnal trips, corresponding to a peak in morning departures and subsequent early evening arrivals, and 2) overnight trips, in which most birds departed in the evening, remained at sea overnight and completed their foraging trip the following morning. Because diurnal and overnight foragers exhibited overlap in the timing of their departures from and arrivals to the island, the midpoint of the foraging trip proved more useful in discriminating the two general strategies and other patterns that might exist. Graphical analysis of the midpoints and durations of trips (1993, Figure 3; 1994, Figure 4) revealed the presence of second category of overnight trips which were initiated before noon, spanned the remainder of the day and into the night, and were terminated the following morning. Overnight trips were categorized as either standard overnight trips, corresponding to the dominant pattern of evening departures followed by morning arrivals, or extended overnight trips, an intermittent pattern in which birds departed in the morning and arrived the following

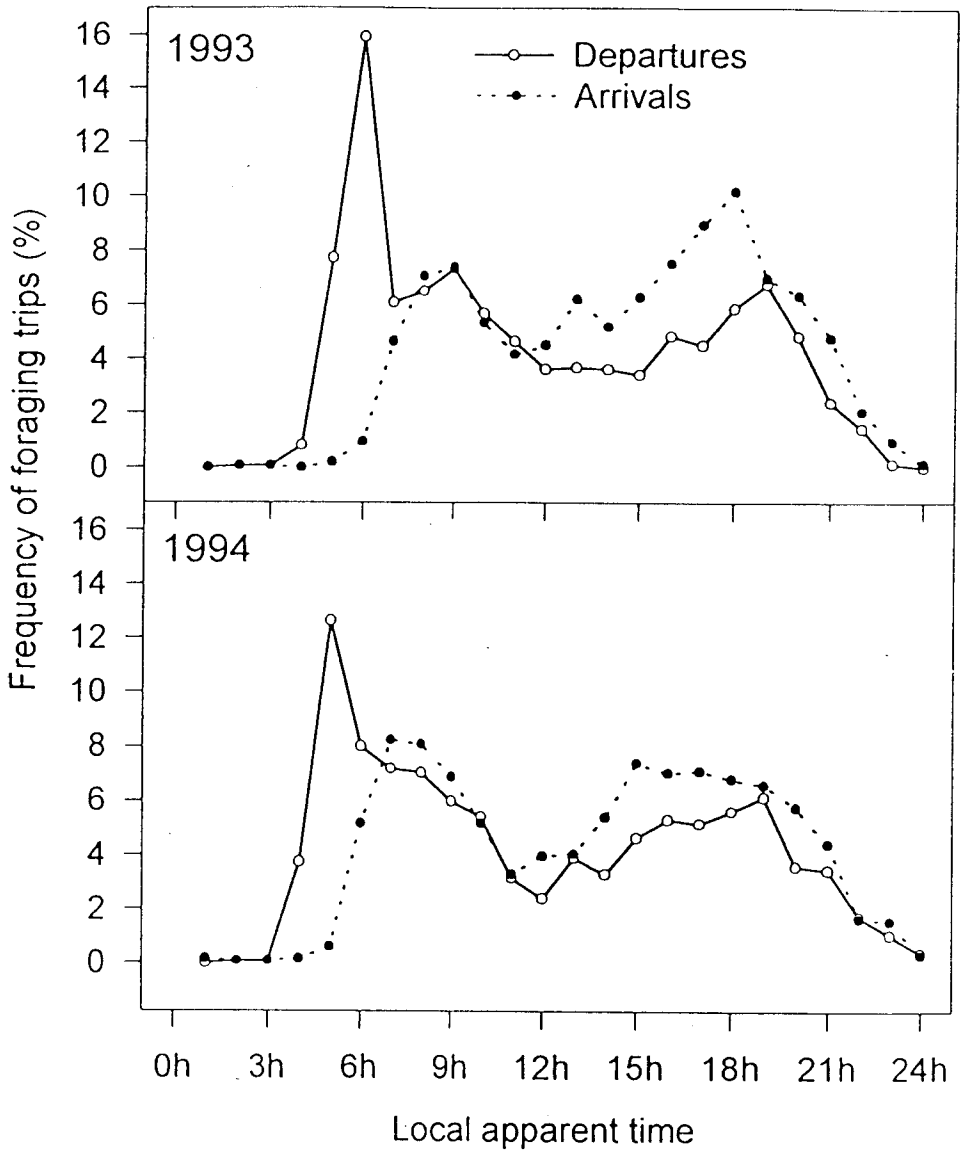

Figure 2. Frequency distribution of Chinstrap Penguins departing from and arriving at North Cove colony, Seal Island in relation to time of day.

morning. Hence, for purposes of analysis, diurnal trips were defined as those being initiated and terminated on the same day, standard overnight trips as those being terminated on the day after the departure date, and extended overnight trips as those overnight trips that were initiated before noon.

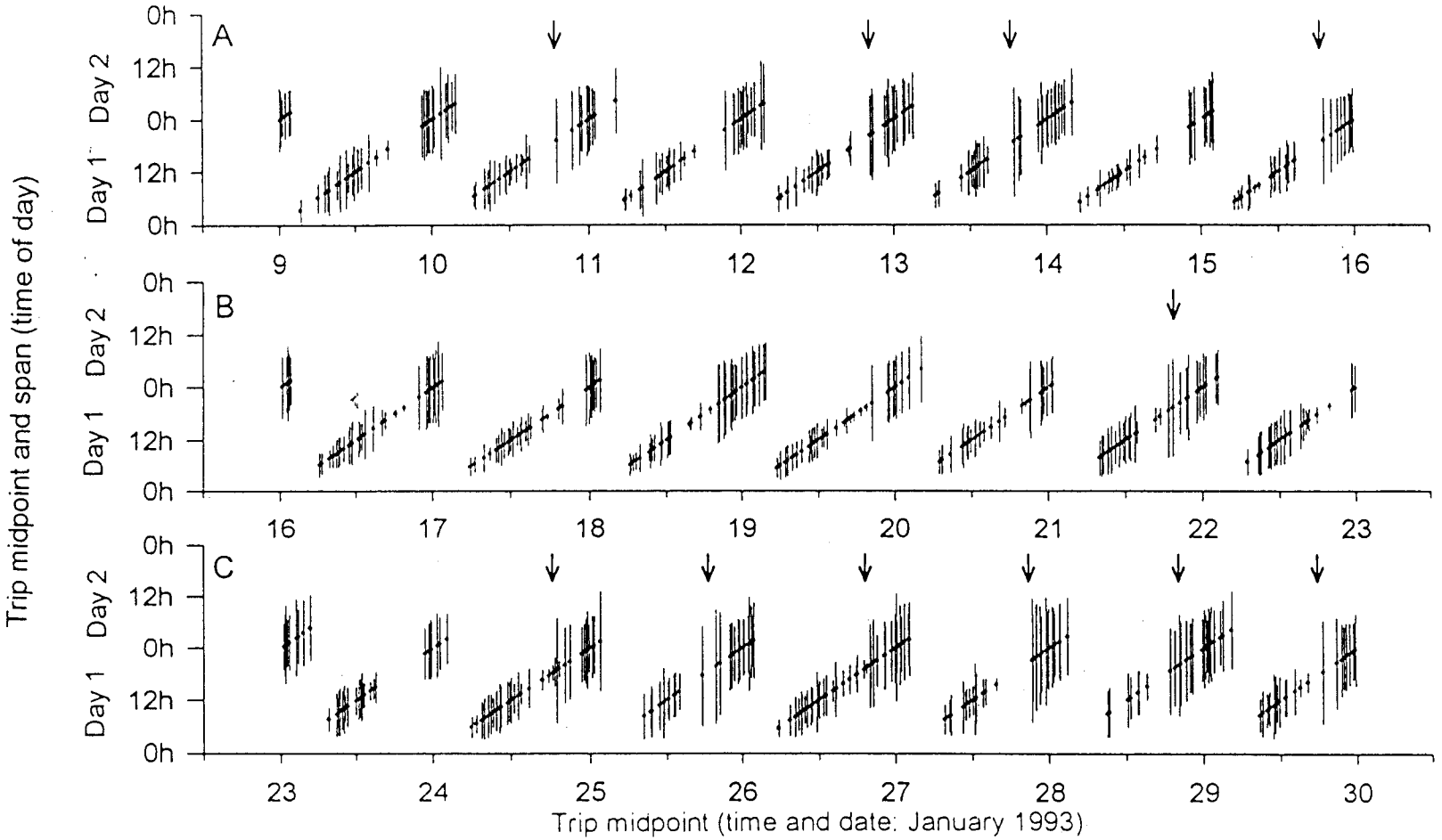

Figure 3. Midpoint (•) and span (vertical lines) of each foraging trip, on the scale of a single foraging cycle (y axis) versus the midpoint on a scale of days (x axis) for A) 9-15 January, B) 16-22 January, and C) 23-29 January 1993. By definition, trips completed on the day they were initiated (span entirely within day 1) are diurnal trips. Overnight trips extend into the following day (day 2). The clusters of data centered near midday reflect diurnal trips and those centered near midnight reflect standard overnight trips. A third category, termed extended overnight trips and marked by arrows in the figure, comprises trips initiated before noon and terminated the following morning.

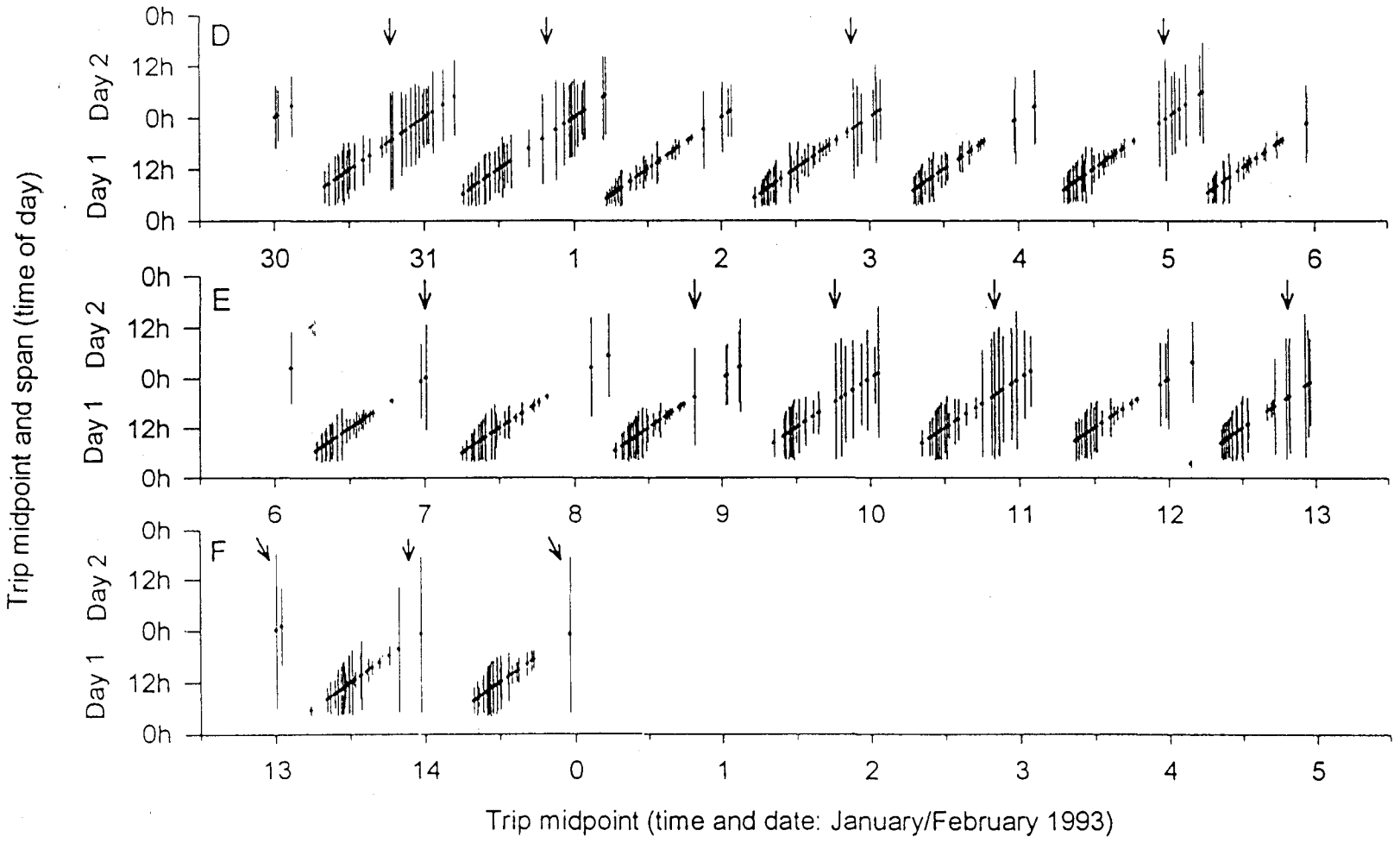

Figure 3-continued. Midpoint (•) and span (vertical lines) of each foraging trip, on the scale of a single foraging cycle (y axis) versus the midpoint on a scale of days (x axis) for D) 30 January -5 February, E) 6-12 February, and F) 13-14 February 1993. For explanation see first part of figure on previous page.

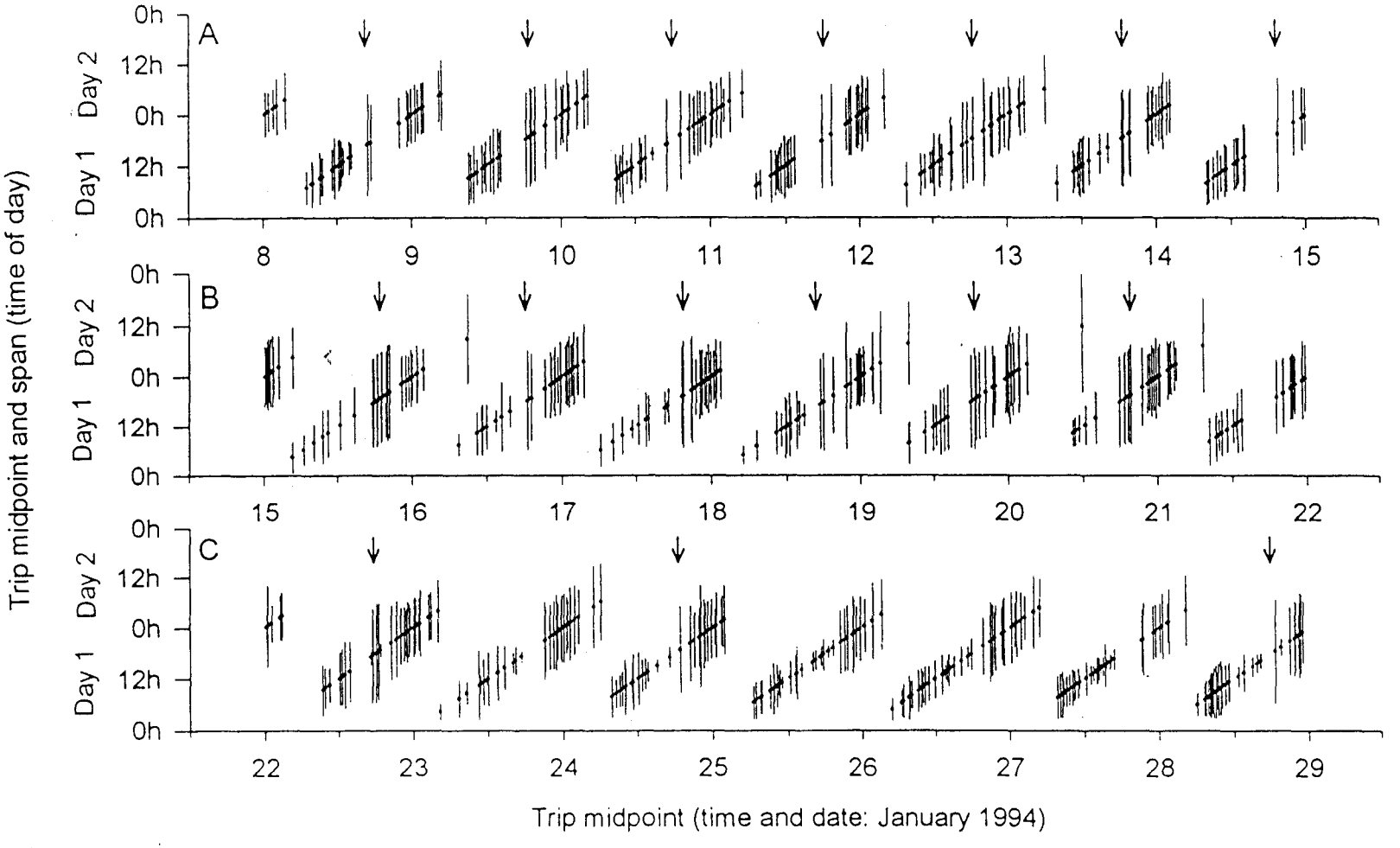

Figure 4. Midpoint (●) and span (vertical lines) of each foraging trip, on the scale of a single foraging cycle (y axis) versus the midpoint on a scale of days (x axis) for A) 8-14 January, B) 15-21 January, and C) 22-28 January 1994. For explanation see Figure 3.

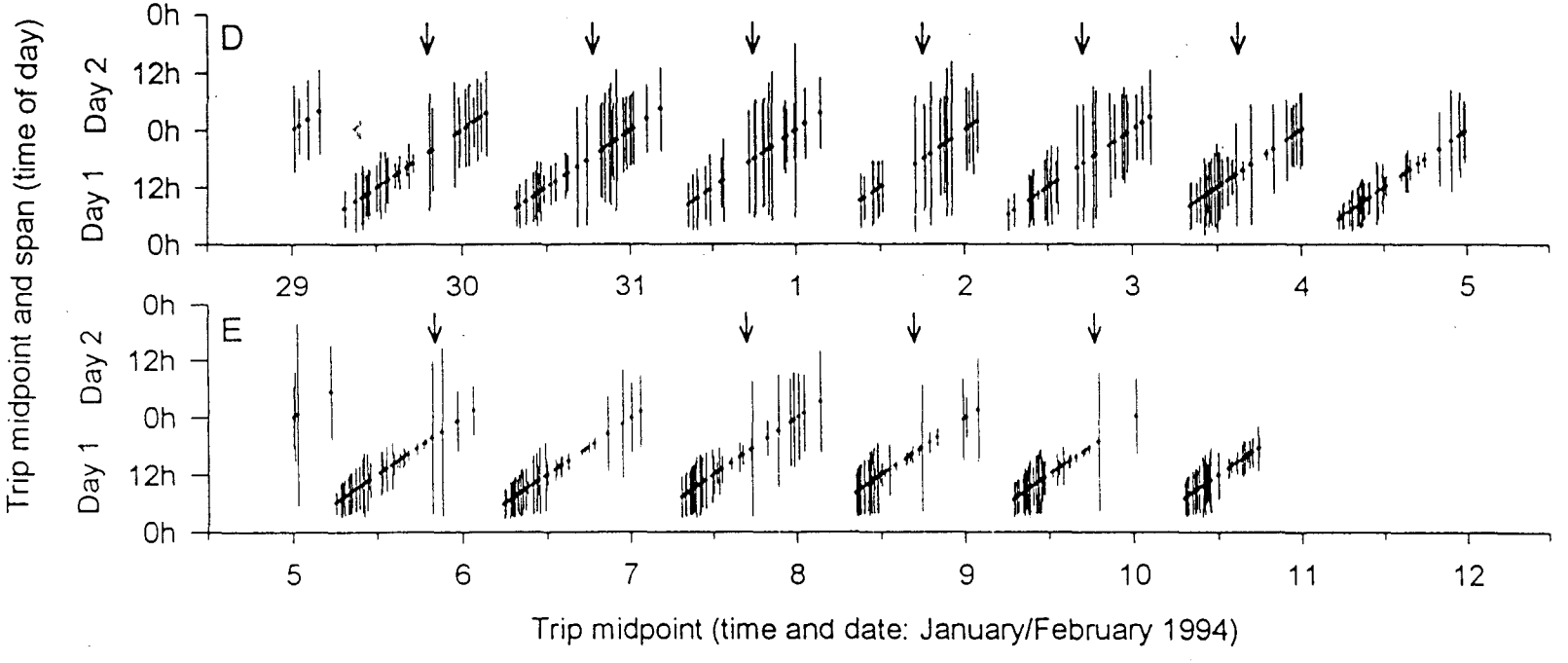

Figure 4-continued. Midpoint (•) and span (vertical lines) of each foraging trip, on the scale of a single foraging cycle (y axis) versus the midpoint on a scale of days (x axis) for D) 29 January - 4 February and E) 5-10 February 1994. For explanation see Figure 3.

Foraging trips were also divided seasonally into three periods that reflected distinct phases of the Chinstrap Penguins' breeding cycle: 1) chick brooding, which extended from the beginning of the study in each year to the day before the first chick in the study nests creched (1993, 9 - 22 January; 1994, 8 - 19 January), 2) transition, defined as the period from the first observed creche to the day 95 % of chicks in the study have creched (1993, 23 January - 1 February; 1994, 20 January - 1 February), and 3) creche, the period during which, for all practical purposes, all nests are in the creche phase (in each year only one nest had chicks that creched after transition), ending upon the beginning of fledging (1993, 2 - 14 February; 1994, 2 - 10 February).

Daily Foraging Patterns

In both years, the most common daily foraging pattern was a single diurnal trip and one standard overnight trip was the second most common (Table 1). Extended overnight trips, two diurnal trips, or coupling a diurnal trip with a standard overnight trip were the next most common patterns, totaling about 20% of the overall daily activity in each year. Birds not taking foraging trips amounted to about 10% of the daily activity in each year. Other multiple trip patterns comprised less than 1% of the overall activity in both years and were excluded from intra- and interannual comparisons of activity patterns.

The overall activity pattern differed between breeding periods and years. During chick-brooding in 1993, one diurnal trip per day was most common, whereas in 1994 the highest percentage of birds completed one standard overnight trip per day. Extended overnight trips were also more common during chick-brooding in 1994 than in 1993

Table 1. Percent frequency of occurrence of types of daily foraging activity patterns (NT = no trip taken, D = diurnal trip, SN = standard overnight trip, EN = extended overnight trip) for Chinstrap Penguins during the breeding season. Two types of trips separated by a comma indicate that both types were initiated by a bird on a given day. Trip designators preceded by a number (x) indicate that this type of trip occurred (x) number of times on a given day. Bird-days represents the total number of days on which individual birds included in the sample were known to takes trips to sea (e.g., 40 birds each foraging over a period of 10 days = 400 bird-days). The distributions of activity patterns were significantly different between all periods. $^{\Psi}$

			Daily foraging activity patterns (%)									Trips · bird · day $^{-1}$
Year	Breeding period	n (bird-days)	D	SN	EN	D, SN	D, EN	2D	2D, SN	3D	NT	
1993	Chick-brooding (9-22 Jan)	556	47.1	31.8	2.5	7	0	2.5	0	0	9	1.00
	Transition (23 Jan - 1 Feb)	390	44.6	27.9	7.2	5.1	0	2.6	0	0.3	12.3	0.96
	Creche (2 Feb - 14 Feb)	472	60.6	5.1	6.8	3	0.2	15.5	0	0.8	8.1	1.12
	Periods combined	1418	50.9	21.9	5.2	5.1	0.1	6.8	0	0.4	9.6	1.03
1994	Chick-brooding (8-19 Jan)	466	33.7	40.6	12	0.9	0	0.2	0.2	0	12.4	0.89
	Transition (20 Jan - 1 Feb)	494	39.1	31	11.1	6.5	0	2	0.2	0	10.1	0.99
	Creche (2 Feb - 10 Feb)	337	53.1	5.3	5	6.2	0	24.9	0.6	0.3	4.5	1.28
	Periods combined	1297	40.8	27.8	9.9	4.4	0	7.3	0.3	0.1	9.5	1.03

$^{\Psi}$ Statistics: Patterns comprising < 1% of the total activity were not included in the comparisons. For each pairwise comparison of activity patterns between periods and years the critical $\Sigma\chi^2$ value = 11.07, df = 5. For the frequency of activity patterns in 1993 and 1994, χ^2= 42.9 and 275.0 for chick-brooding vs. transition, 489.2 and 9942.1 for chick-brooding vs. creche, and 436.6 and 990.4 for transition vs. creche, respectively; for inter-annual comparisons, χ^2= 237.7, 20.0, 41.6 for the three periods, and 102.4 for periods combined, respectively. All $P < 0.0001$.

(Table 1). During transition phase in both years, birds took mostly single diurnal trips. However, birds completing any overnight trip (i.e., standard and extended overnight trips combined) during transition in 1994 were still slightly more common than those taking a diurnal trip. The foraging patterns of penguins during creche were similar between the two years with most birds completing one or two diurnal trips per day with standard overnight trips becoming relatively infrequent (Table 1).

A chi-square analysis revealed that the frequencies of these daily foraging patterns were significantly different between periods and years ($p < 0.001$ for each pair-wise comparison; critical value for $\Sigma\chi^2 = 11.07$ with $df = 5$; Table 1). Partitioning $\Sigma\chi^2$ determined which activity patterns contributed most to the differences. In 1993, the change in activity patterns when progressing from chick-brooding to transition was mostly attributed to an increase in the frequency of birds taking one extended overnight trip ($\chi^2 = 33.8$). However, extended overnight trips were not very common compared to the dominant pattern of most birds taking either one diurnal or standard overnight trip per day. The shift in activity patterns between transition and creche was primarily due to a decline in standard overnight trips and an increase in birds taking two diurnal trips (Table 1; $\chi^2 = 87.3$ and 309.9, respectively). This trend was also evident over the entire study period ($\chi^2 = 104.5$ and 318.9, respectively, for chick-brooding versus creche).

In 1994, the change in activity between chick-brooding and transition was mostly the result of an increase in birds that took two trips per day; either two diurnal or one diurnal trip and one standard overnight trip per day (Table 1; $\chi^2 = 181.7$ and 75.4, respectively) but again these patterns were not common, amounting to less than 10% of

the total activity. Similar to 1993, significant changes that occurred between transition and creche were largely attributed to an increase in the incidence of birds taking two diurnal trips per day ($\chi^2 = 880.3$) and a decrease in birds completing standard overnight trips ($\chi^2 = 70.8$). As in the previous year, the increase in the incidence of birds taking two trips per day was largely responsible for the differences that occurred over the entire period in 1994 (Table 1; two diurnal trips, $\chi^2 = 9656.2$; one diurnal trip & one standard overnight trip, $\chi^2 = 114.4$). A decrease in birds taking standard overnight trips was also important in differences between chick-brooding and creche ($\chi^2 = 102.1$).

The relative frequency of foraging patterns also changed significantly between 1993 and 1994 within each breeding phase (Table 1). Differences between years in both the chick-brooding and transition periods were primarily attributed to more birds taking extended overnight trips in 1994 ($\chi^2 = 167.5$ and 19.4, respectively). An increased incidence of birds taking one diurnal trip combined with a standard overnight trip, and birds taking just one diurnal trip per day in 1993 also contributed to differences during chick-brooding between years ($\chi^2 = 25.1$ and 17.6, respectively). Comparisons of the creche phase showed that differences were mostly attributed to more birds completing two diurnal foraging trips per day in 1994 ($\chi^2 = 19.4$). Interannual comparisons of foraging patterns for all periods combined indicate that 1993 was characterized by fewer birds taking extended or standard overnight trips ($\chi^2 = 53.7$ and 20.5, respectively) and more birds taking one diurnal trip per day ($\chi^2 = 26.2$) relative to 1994.

Individual Foraging Behavior

In 1993 and 1994, diurnal foraging trips comprised, on average, more than half of a bird's trips to sea with the remainder being either standard or extended overnight trips (Table 2.). No penguins exhibited a strict specialization on one type of foraging trip

Table 2. Mean percent trip frequency (S.E.) for Chinstrap Penguins taking diurnal (D), standard overnight (SN), extended overnight (EN) trips. Mean frequencies are the incidence of a type of trip averaged across the means of individual birds during the specified breeding phase (i.e., n = birds). Birds that did not complete trips during each of the breeding phases were not included in the periods combined summary.

	Types of Foraging Trips (%)							
	1993				1994			
Breeding period	n	D	SN	EN	n	D	SN	EN
Chick-brooding	40	59 (25)	38 (25)	3 (4)	39	40 (26)	46 (30)	14 (13)
Transition	39	58 (28)	34 (28)	8 (9)	38	50 (24)	38 (25)	12 (8)
Creche	39	84 (16)	8 (10)	8 (9)	38	86 (15)	9 (14)	5 (7)
Periods combined	39	68 (15)	26 (14)	6 (5)	38	59 (14)	31 (16)	10 (7)

throughout the study period in either year (Figures 5 and 6, respectively). However, in 1993 during chick-brooding and creche, 8% and 21% of birds, respectively, foraged exclusively during the day (Figure 5). In 1994, there were no diurnal specialists during chick-brooding while 32% of the birds foraged solely by day during creche (Figure 6). Although strict diurnal specialization during a breeding period was generally rare, 85% of the birds in 1993 and 76% in 1994 exhibited diurnal foraging on more than half of their

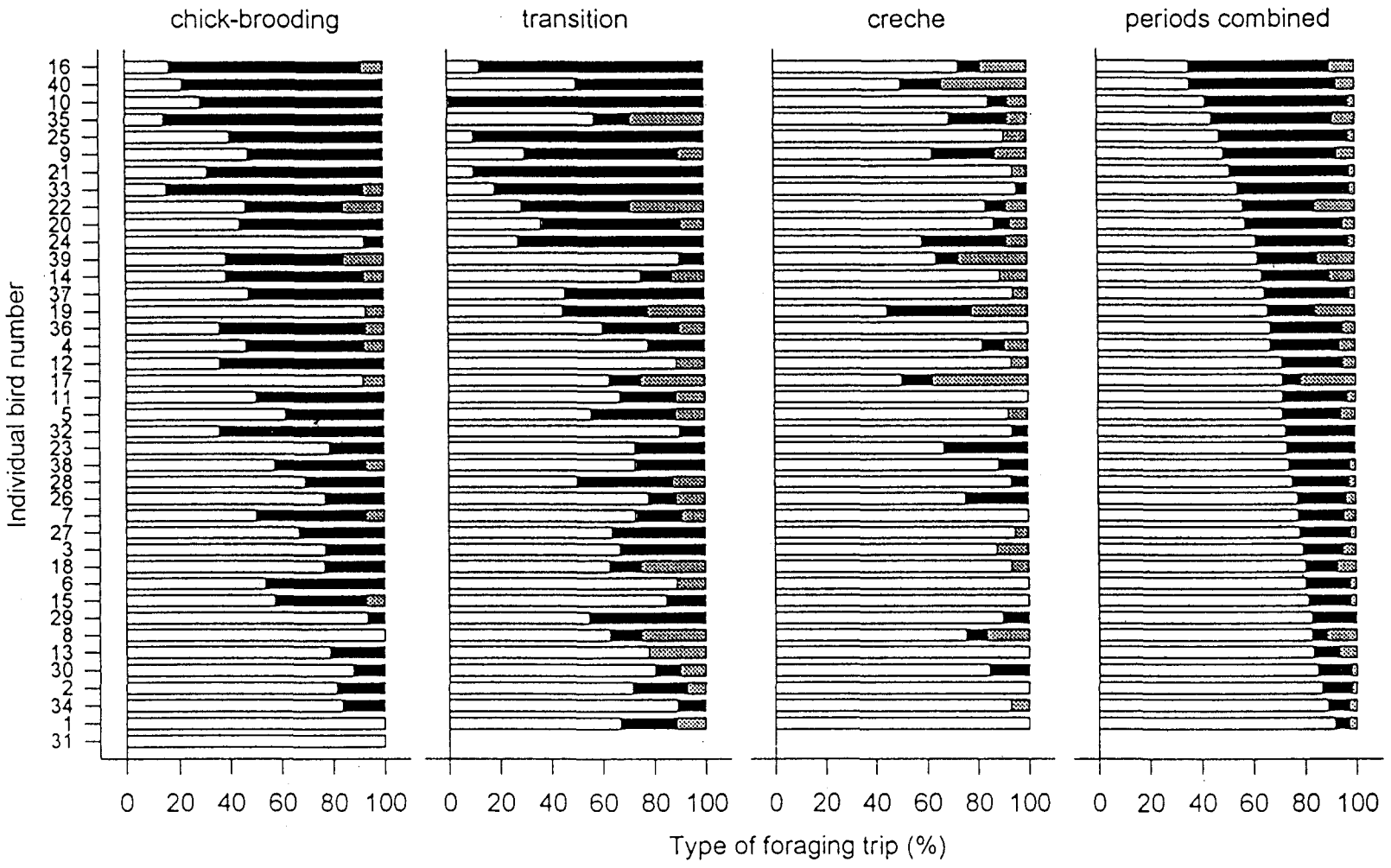

Figure 5. Incidence of diurnal (□), standard overnight (■), and extended overnight (▨) foraging in individual penguin's foraging behavior during each of the specified breeding periods and for periods combined in 1993. Birds are organized in order of increasing overall frequency of diurnal foraging trips from top to bottom.

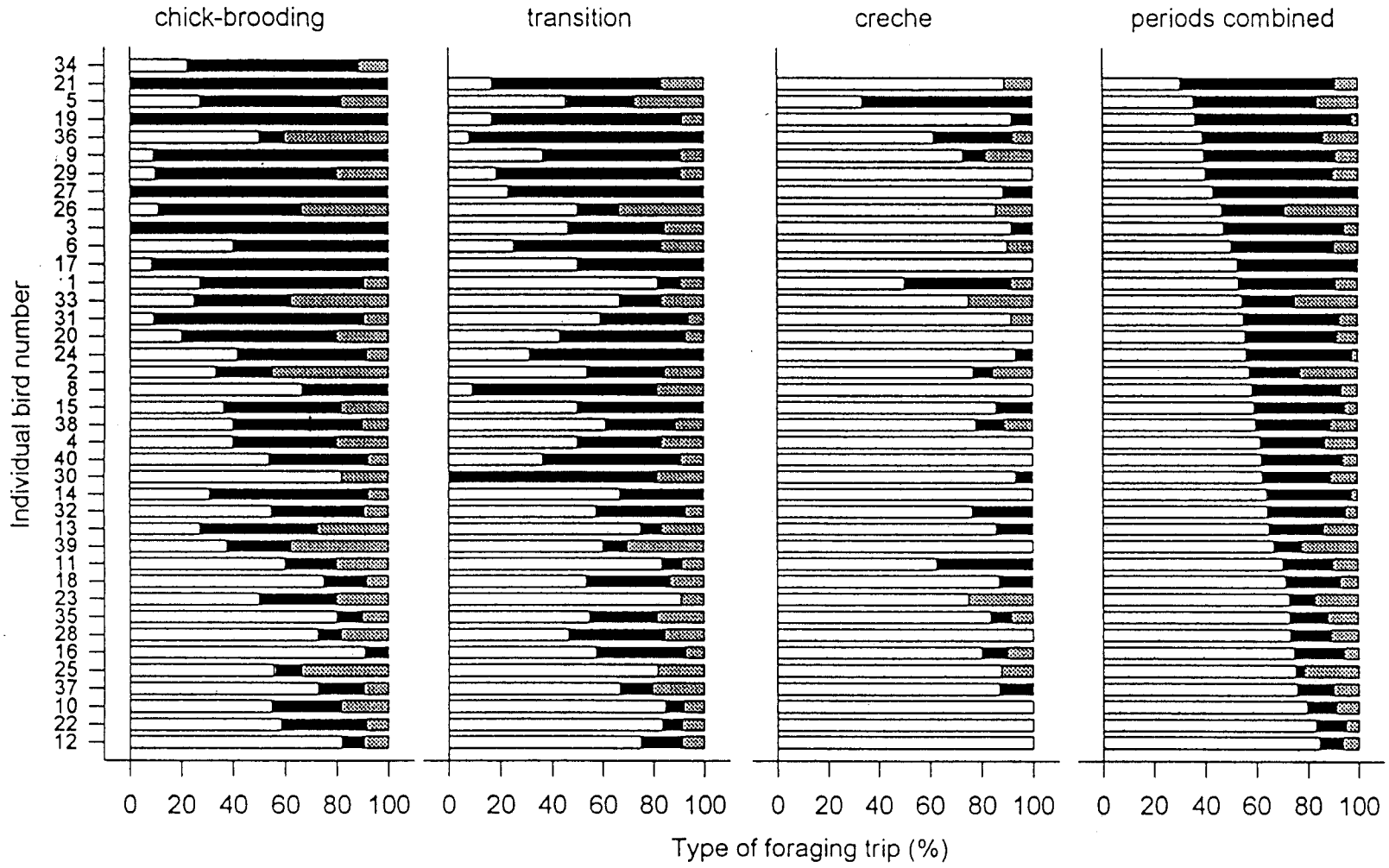

Figure 6. Incidence of diurnal (□), standard overnight (■), and extended overnight (▤) foraging in individual penguin's foraging behavior during each of the specified breeding periods and for periods combined in 1994. Birds are organized in order of increasing overall frequency of diurnal foraging trips from top to bottom.

trips during the study period. A small percentage of birds did forage only at night during certain periods; in 1993, 3% during transition and in 1994, 10% during chick-brooding and 3% during transition.

Pattern of Arrivals and Departures

The frequency distributions of arrival and departure times, presented in Figure 2, also reflect the changes in the relative importance of types of foraging between periods and years (1993, Figure 7; 1994, Figure 8). Because penguins often initiated two trips in a day, the arrivals and departures of diurnal and standard overnight trips as either first or second trips of the day were considered separately. In general, penguins traveled to and from the island only during daylight hours, very little activity being exhibited at night. During the entire study period in 1993 and 1994 only 1% and 6% of diurnal trips, respectively, were initiated before sunrise and only 2% and 3% terminated after sunset. This lack of activity at night was also evident in departures on standard overnight foraging trips, of which only 1% and 19% occurred after sunset in 1993 and 1994, respectively. Less than 1% of the subsequent arrivals occurred before sunrise in both years.

Arrivals and Departures in 1993

Diurnal Trips

Patterns of arrivals and departures for penguins taking diurnal foraging trips were similar during chick-brooding and transition in 1993 (Figure 7; 1a, 2a). During both

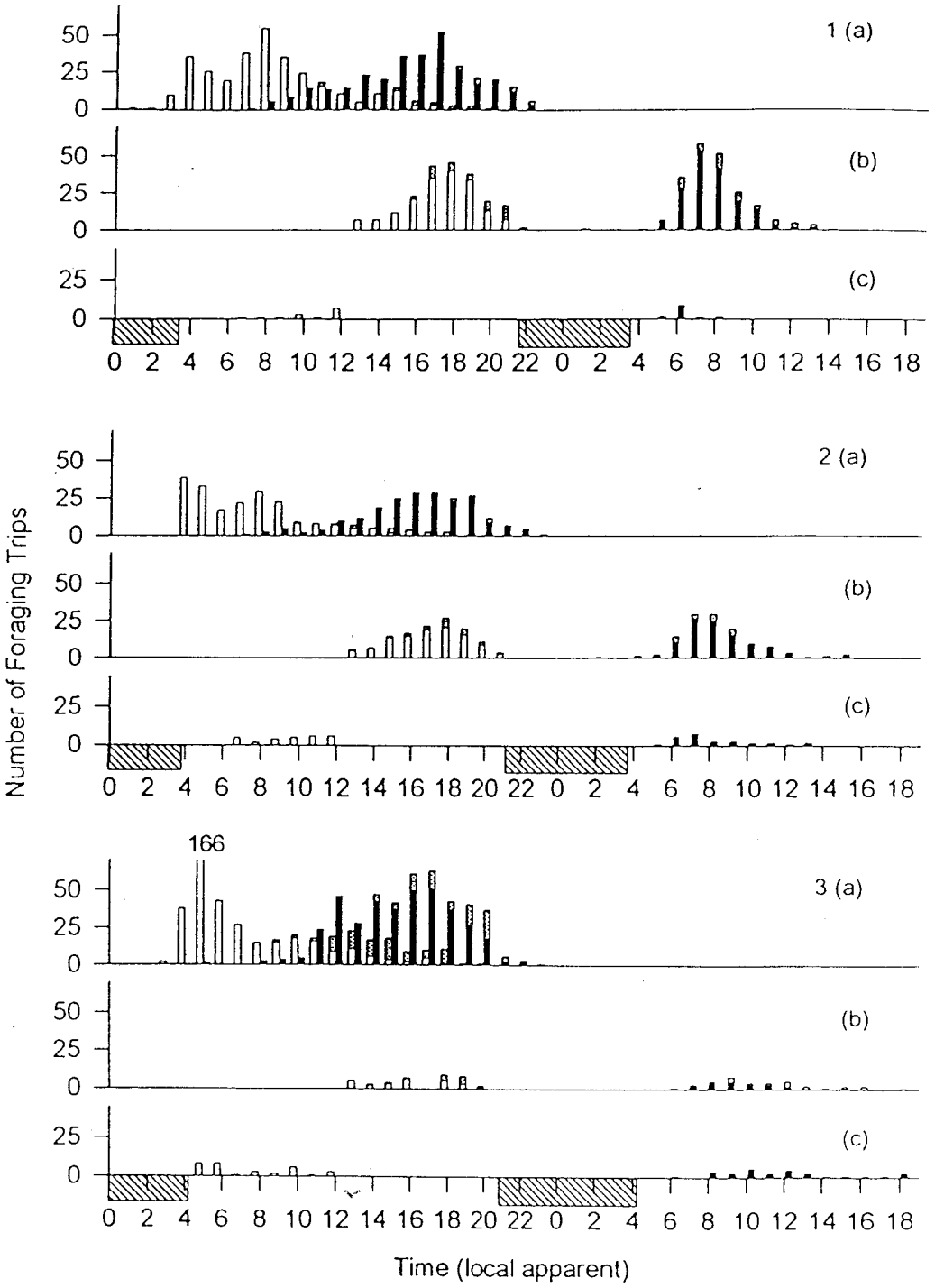

Figure 7. Distribution of departure (□) and arrival (■) times of Chinstrap Penguins for a) diurnal, b) standard overnight, and c) extended overnight foraging trips during 1) chick-brooding, 2) transition, and 3) creche in 1993. Stippled bars indicate those trips that were taken as the second trip initiated on a given day. Shading on the time axis shows the period between sunset and sunrise.

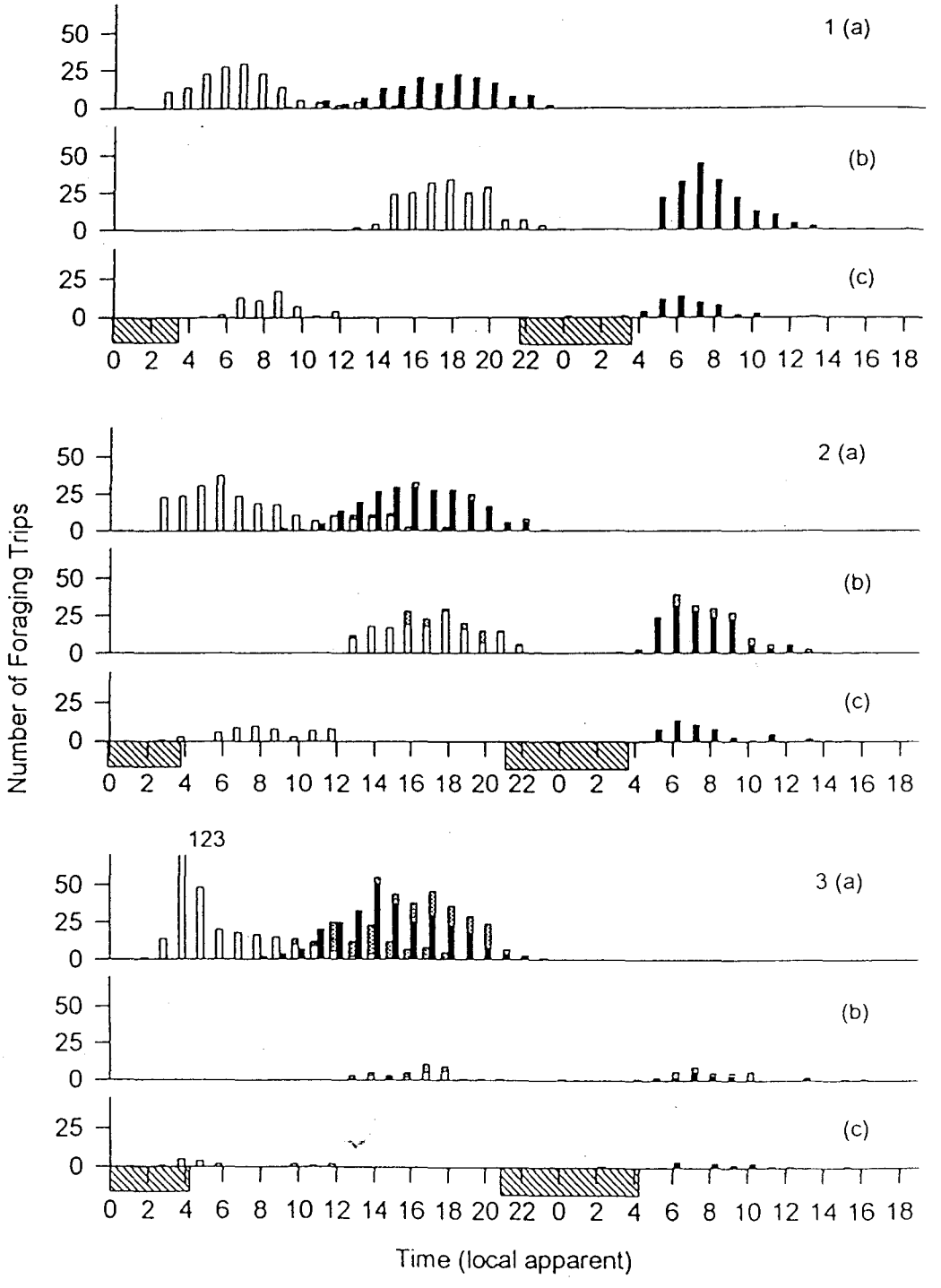

Figure 8. Distribution of departure (□) and arrival (■) times of Chinstrap Penguins for a) diurnal, b) standard overnight, and c) extended overnight foraging trips during 1) chick-brooding, 2) transition, and 3) creche in 1994. Stippled bars indicate those trips that were taken as the second trip initiated on a given day. Shading on the time axis shows the period between sunset and sunrise.

periods, more than 70% of birds initiating diurnal foraging trips left between 0300 h and 1000 h and arrived back between 1200 h and 2000 h. During chick-brooding, diurnal trip departures increased at 0400 h and later peaked in higher numbers at 0800 h (Figure 7; 1a). Low numbers of departures continued until about 2000 h; 10% of departures after the 0800 h mode represented second diurnal trips. As the birds progressed into the transition period the timing of departures remained bimodal, but the relative importance of the modes switched, with the 0400 h mode becoming more pronounced than the peak at 0800 h (Figure 7; 2a). During the creche period, this bi-modal distribution of departures was replaced by a single pronounced peak at 0500 h, during which more than a third of the birds departed (Figure 7; 3a). Birds taking a second diurnal trip contributed to a minor mode at about 1300 h; 47% of departures after 0800 h represented second diurnal trips. Arrivals during creche reflected this bimodal pattern of departures in having at least two peaks: one at 1100-1300 h, composed solely of birds completing their first diurnal trip of the day followed by a more prominent mode at around 1500-2000 h, which was composed both of birds completing their first (77%) and second (23%) diurnal trips of the day.

Standard Overnight Trips

Birds departing on standard overnight trips also showed similar patterns between chick-brooding and transition with at least three-quarters of birds departing between 1500 h and 2000 h (79% and 75%, respectively) and arriving back between 0500 h and 1000 h the following morning (88% and 81%; Figure 7; 1b, 2b). There appears to be no difference in the timing of arrivals and departures between birds making their first or

second trips of the day during chick-brooding and transition. Although fewer trips were taken during creche, it appears that birds began departing in two waves: one at around 1200-1600 h (n=19 trips), which mostly corresponded to birds' first trip of the day (84%), and another at 1700-2000 h (n=19 trips), which was largely composed of birds taking their second trip of the day (59%; Figure 7; 3b). The distribution of arrivals during creche was also similar to earlier periods, although slightly more drawn out, with only 55% arriving between 0500 h and 1000 h.

Extended Overnight Trips

Departures on extended overnight trips during chick-brooding and transition appeared similar to the later morning departures of diurnal foraging trips (i.e., 0800 h mode) although the frequency of these trips was very low. These trips were completed within the same time period as standard overnight trips although they tended, on average, to return slightly earlier (Figure 7; 1c, 2c). During creche, while extended overnight foraging was still infrequent, it appeared that most of the departures coincided with the pronounced 0500 peak in diurnal trip departures (Figure 7; 3c). Arrivals during creche occurred over a broader time span, with birds continuing to arrive up to 5 hours after the latest arrival observed in previous periods.

Arrivals and Departures in 1994

Diurnal Foraging Trips

During 1994, the frequency distribution of departures and arrivals for diurnal trips was similar for chick brooding and transition with most birds departing between 0300 h and 1000 h (84% and 66%, respectively) and arriving back between 1200 h and 2000 h (82% and 84%; Figure 8; 1a, 2a). In contrast to 1993, these periods in 1994 each had a single mode of departures with that of transition (0600 h) being an hour earlier than during chick-brooding (0700 h). Similar to 1993, departures during creche occurred in two modes: a prominent one at 0400 h, during which almost a third of the birds departed, and a later one at 1100-1400 h, which corresponded mostly to birds taking a second diurnal trip on a day (71%; Figure 8; 3a).

Standard Overnight Trips

As in 1993, most birds departing on standard overnight trips during chick-brooding, transition, and creche in 1994 left between 1500 h and 2000 h (75%, 63%, and 68%, respectively) and arrived back between 0500 h and 1000 h (76%, 74%, and 78%; Figure 8; 1b, 2b, 3b). The frequency of birds taking standard overnight trips again decreased through the season. Similar to 1993, there appeared to be no dependence, in timing of these trips, on whether they were initiated as the first or second trip of the day. The majority of birds that continued to take standard overnight trips during creche did so only after taking another trip earlier in the day (Figure 8; 3b).

Extended Overnight Trips

All extended overnight trips during chick-brooding and transition were initiated within the time period of departures for diurnal foraging trips but appeared to be shifted slightly later (Figure 8; 1c, 2c). During chick-brooding and transition, as in 1993, arrivals appeared to conform to those of standard overnight foraging trips. However, extended overnight trips during chick-brooding appeared to be terminated slightly earlier on average than standard overnight trips (Figure 8; 1c). Similar to 1993, the majority of departures during creche occurred during the primary mode of diurnal departures (0400 h) with arrivals being comparable as well.

Duration of Foraging Trips

Penguins foraged for significantly different amounts of time within each year depending on the type of trip taken (ANOVA, 1993, $F_{4, 173} = 333.3$, $P < 0.0001$; 1994, $F_{4, 167} = 503.8$, $P < 0.0001$), but trip duration was not different between years ($F_{1, 341} = 0.12$, $P = 0.73$). For this analysis, diurnal and standard overnight trips were again divided depending on whether the trip was the first or second trip of the day. Results of multiple comparisons within each year revealed that all types of trips were of significantly different durations (all $P < 0.05$) except the two types of standard overnight trips (SN_1, SN_2; Table 3). In general, first and second diurnal trips were shortest, standard overnight trips were intermediate, and extended overnight trips were longest (Table 3). First diurnal trips were about 40% shorter, on average, than standard overnight trips, which were about

two-thirds the duration of extended overnight trips making first diurnal trips less than half the duration of extended overnight trips (all $P < 0.05$). Second diurnal trips were the shortest being less than half the length of first diurnal trips ($P < 0.05$). Because the two basic types of overnight trips were distinguished based on whether the trips were initiated before or after noon, a somewhat arbitrary point, the statistical comparisons of trip duration between the two should be treated with caution.

Table 3. Mean foraging trip durations (hours (S.D.); n = birds) for Chinstrap Penguins taking diurnal (D_1), second diurnal (D_2), standard overnight (first trip of the day; SN_1), standard overnight (second trip of the day; SN_2), and extended overnight (EN) foraging trips for all breeding periods combined.

	1993		1994	
Type	n (no. of trips)	Trip duration	n (no. of trips)	Trip duration
D_1	40 (898)	8.5 (1.2)	39 (685)	9.2 (1.2)
D_2	31 (102)	3.9 (1.3)	28 (100)	3.9 (0.95)
SN_1	39 (310)	14.8 (1.9)	39 (360)	14.5 (2.7)
SN_2	29 (73)	13.9 (2.3)	25 (57)	15.4 (2.6)
EN	35 (74)	24.2 (4.2)	37 (128)	22.8 (2.3)

Effect of Departure Time on Duration of Foraging Trips

Foraging trip duration decreased with time of departure for each type of foraging trip with all slopes being highly significant ($P < 0.0001$) in both years (Figure 9). Parameters of the linear regression analysis for 1993 and 1994 are presented in Table 4. A two-way ANCOVA with departure time as the covariate indicated that the effect of

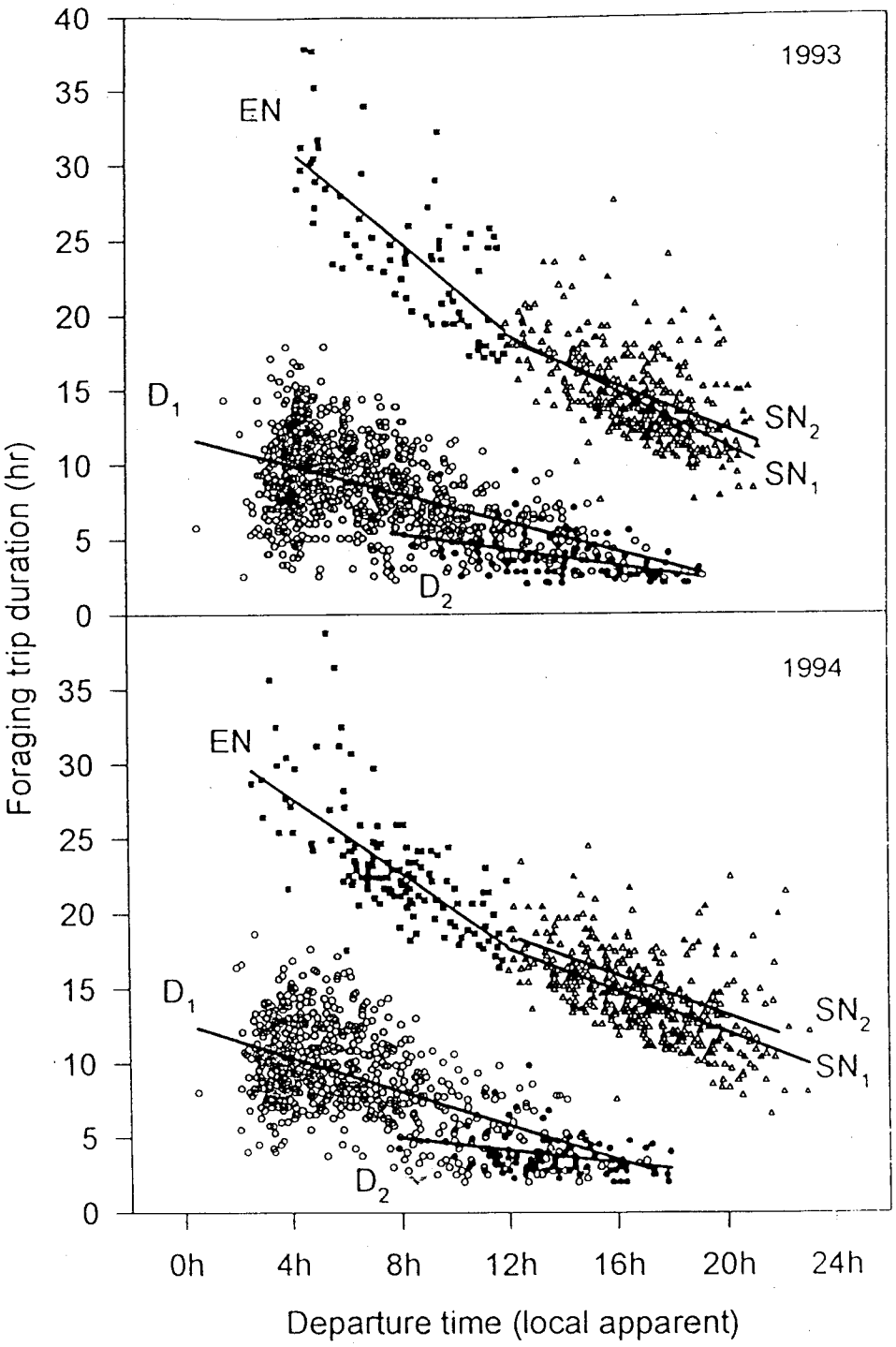

Figure 9. Relationship between foraging trip duration and time of departure in breeding Chinstrap Penguins during 1993 (upper) and 1994 (lower); determined for diurnal trips (D_1-O, D_2-●), standard overnight trips (SN_1-Δ, SN_2-▲) and extended overnight trips (EN-■). Refer to Table 4 for explanation of trip abbreviations and regression statistics.

departure time on foraging trip duration varied significantly between types of trips ($F_{4, 2786}$ = 168.2, $P < 0.001$) but that this effect did not vary between years ($F_{1, 2786} = 0.1$, $P = 0.98$). Multiple pair-wise ANCOVAs were used to determine whether the slopes differed between types of trips within each year. These analyses revealed the same trend in both years. The magnitude of the effect of departure time on foraging trip duration was greater for overnight trips than for diurnal trips with one exception: first diurnal trips did not differ from the relatively uncommon standard overnight trips taken as the second trip of the day (Table 4). First and second standard overnight trips were also not different ($P > 0.25$ in both years). The slope was steepest among extended overnight trips ($P < 0.01$ for all pair-wise comparisons; Figure 9) indicating that birds arriving after extended overnight trips did so within a narrower window, relative to a broad range of departures, than other

Table 4. Linear regression statistics for the relationship between foraging trip duration (y) and departure time (x) for diurnal trips (D_1 and D_2), standard overnight trips (SN_1 and SN_2), and extended overnight trips (EN). Trip type designations are as described in Table 3.

	Linear regression statistics							
	1993				1994			
Trip type	b	b(0)	r^2	y/x (minutes) [a]	b	b(0)	r^2	y/x (minutes) [a]
D_1	0.48	11.92	0.26	29	0.57	12.64	0.30	34
D_2	0.26	7.41	0.20	16	0.21	6.67	0.10	13
SN_1	0.92	29.75	0.38	55	0.69	25.97	0.34	42
SN_2	0.74	27.16	0.21	44	0.67	26.58	0.24	40
EN	1.53	37.29	0.54	92	1.25	32.85	0.49	75

[a] This statistic provides an index showing how much shorter specified foraging trips are for every 60 minutes trips were delayed (e.g., D_1 trips in 1993 were 29 minutes shorter, on average, for each hour later those trips were initiated).

types of trips. In fact, birds that were among the last to depart on extended overnight trips were among the first to arrive the next day. The least influence of departure time on foraging duration was observed in second diurnal trips, during which birds tended to forage for 3-10 hours irrespective of the time they departed the island ($P = 0.03$ compared with first diurnal trips; $P < 0.001$ for each of the comparisons with overnight trips).

Light Regimes for Foraging Penguins

Foraging penguins experienced, on average, significantly different light levels depending on the type of trip utilized ($F_{4,663} = 58.3$ and $F_{4,1323} = 454.4$ for 1993 and 1994, respectively, $P < 0.0001$ for both years). Multiple comparisons (pairwise between each type of trip; all $P < 0.05$) indicated that in both years birds experienced the highest light levels, on average, during diurnal foraging, with first diurnal trips experiencing significantly more light than second trips only in 1994. Extended overnight trips were generally intermediate being different from all others except second diurnal trips in both years. Light levels experienced during the two types of overnight foraging trips were significantly lower than during other types of trips, but were not different from each other (Figure 10). Birds on first diurnal trips experienced approximately ten times more light (1 $\log_{10}$ lux), on average, than birds on standard overnight trips. There was, however, considerable overlap in the light regimes experienced by individual penguins taking each type of trip.

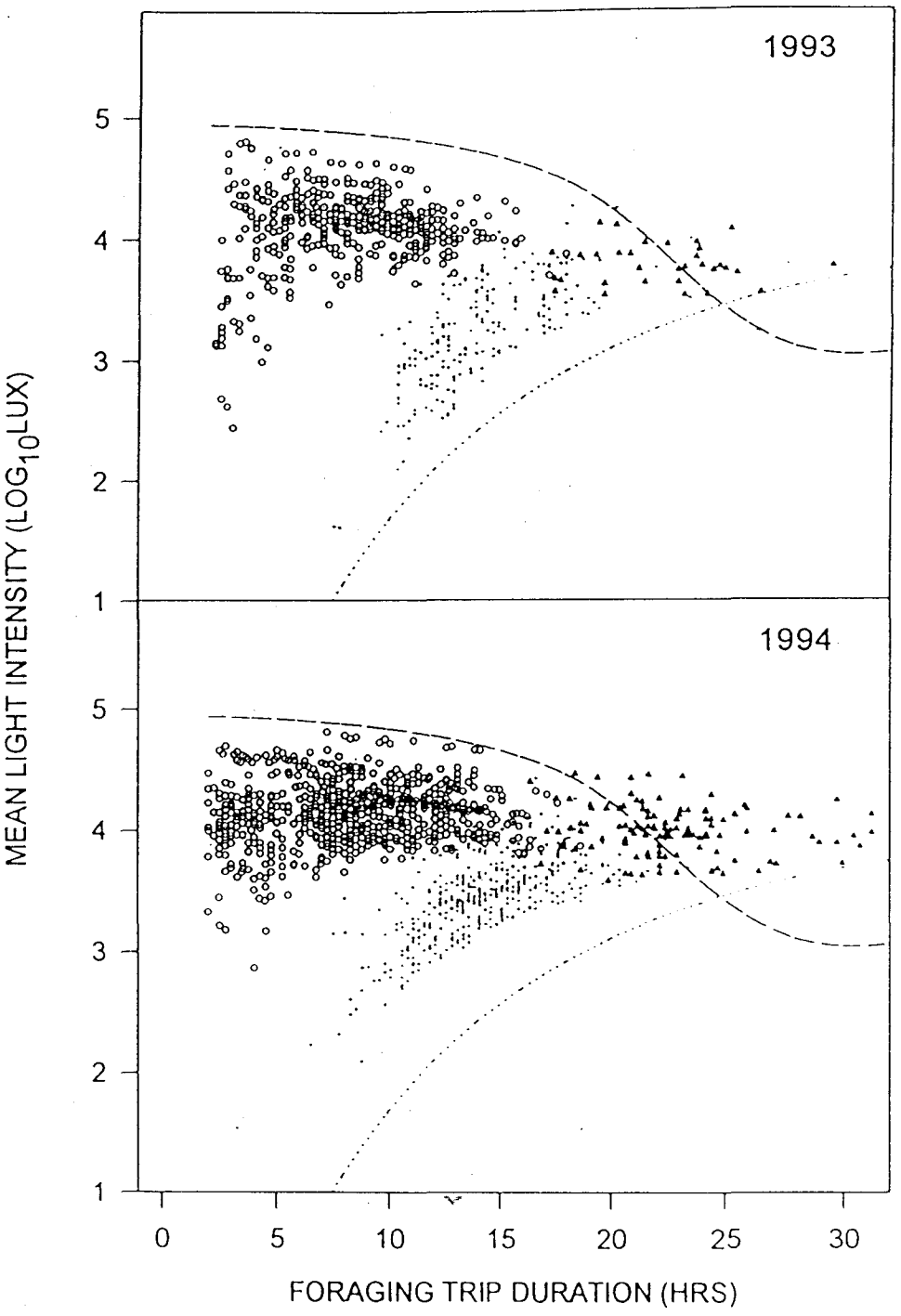

Figure 10. Relationship between mean light intensity calculated per trip and foraging trip duration during 1993 (upper) and 1994 (lower); determined for diurnal (O), standard overnight (•), and extended overnight (▲) foraging trips. Lines illustrate the theoretical upper (– –) and lower (····) limits of light, for trips of varying length, calculated for the first day of the study in each year assuming cloudless conditions.

Effects of Variable Illumination on Duration of Foraging

During the period light levels were sampled in 1993, the duration of first diurnal trips were longer during decreased light levels ($F_{1,16} = 14.69$, $b = -6.19$, $r^2 = 0.51$, $P = 0.002$; Figure 11). The duration of second diurnal trips also tended to increase with decreasing light levels but the trend was not significant ($b = -4.43$, $r^2 = 0.20$, $P = 0.22$). During the entire study period in 1994, light levels apparently did not have an effect on the duration of either first ($b = 0.69$, $r^2 = 0.007$, $P = 0.64$) or second diurnal trips ($b = -2.08$, $r^2 = 0.16$, $P = 0.14$). The effect of light levels on the duration of overnight trips was not assessed due to limitations of the instruments under low light conditions.

Partitioning the regression analysis to examine potential effects of light on trip duration within each breeding period was not possible in 1993 because light sampling was mostly confined to the transition period. Examining each period separately in 1994, did not reveal any significant effect of light on trip duration for any one period. There was, however, a greater tendency toward longer first diurnal trips on darker days during chick-brooding ($b = -3.16$, $r^2 = 0.23$, $P = 0.16$) than later in the season (transition, $b = -0.55$, $r^2 = 0.004$, $P = 0.84$; creche, $b = 0.67$, $r^2 = 0.009$, $P = 0.81$).

Daily and Seasonal Occurrence of Nocturnal Foraging

The daily occurrence of first standard overnight trips and extended overnight trips in relation to the progression of creching and the change in daylength is presented in Figures 12 and 13 for 1993 and 1994, respectively. In both years, there was considerable

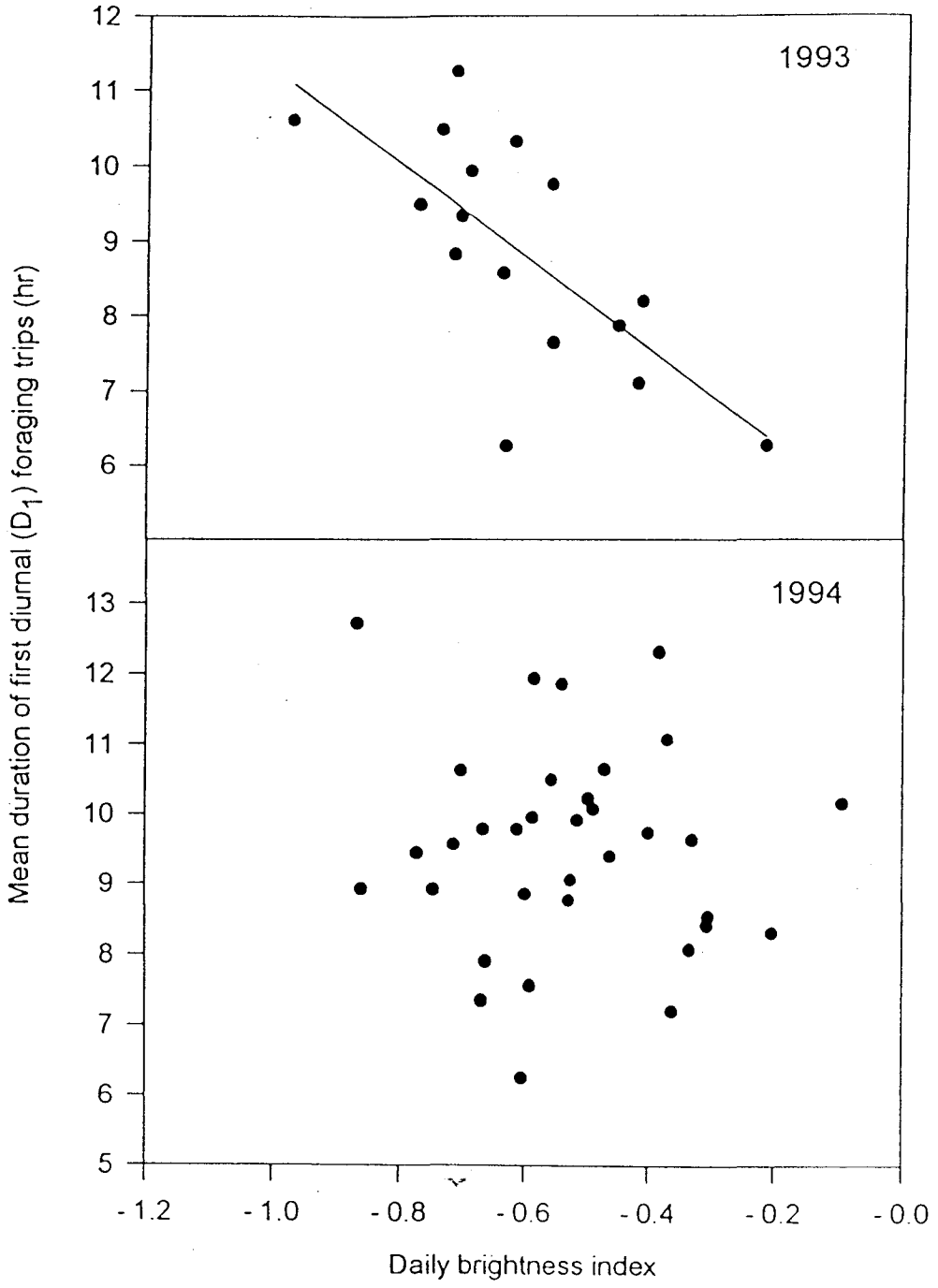

Figure 11. Relationship between daily mean duration of first diurnal foraging trips and brightness index calculated daily for 1993 (upper panel) and 1994 (lower panel). Slope was highly significant in 1993 (P = 0.002) but not in 1994 (P = 0.64).

variability in the occurrence of standard overnight foraging trips within each period, but overall there was a significant decline in their frequency during transition, 4-7 days after the first chicks creched. The daily frequency of extended overnight trips did not show any obvious seasonal trend in either year (Figures 12 and 13), but rather was positively related to the daily mean duration of first diurnal trips (Figure 14; $P < 0.0001$ for both years).

Diet of Diurnal and Overnight Foragers

In 1993 and 1994, all Chinstrap Penguins returning from diurnal and overnight trips had predominantly krill (Euphausia species) in their stomachs (Table 5). Fish was found almost exclusively in birds that had been feeding overnight; only one diurnal sample in 1993 had evidence of fish. While in both years fish was more likely to occur in the stomachs of overnight foragers ($\Sigma\chi^2 = 118.05$ and 269.5, respectively, both $P < 0.001$), fish was more common in 1994 than 1993 ($\Sigma\chi^2 = 10.67$, $P < 0.025$) also occurring in significantly greater numbers (comparison of number of otoliths between years: $t_{1, 23} = 1.97$, $P < 0.035$, Table 5). Remnants of squid and amphipods were observed only rarely composing, on average, less than one percent of the total mass of the diet sample.

Fish occurring in the diet of overnight foragers were never intact and usually in the form of small pieces of flesh, bones and otoliths. The fish prey of overnight foragers, in both years, were primarily lanternfish, family Myctophidae (95%), such as Electrona antarctica, E. carlsbergi, Gymnoscopelus nicholsi, and Krefftichthys anderssoni and less commonly the paralepidid Notolepis coatsi (5%). During lavaging, evidence of fish would appear only after a layer of fresher krill had been regurgitated. In 1993, only one

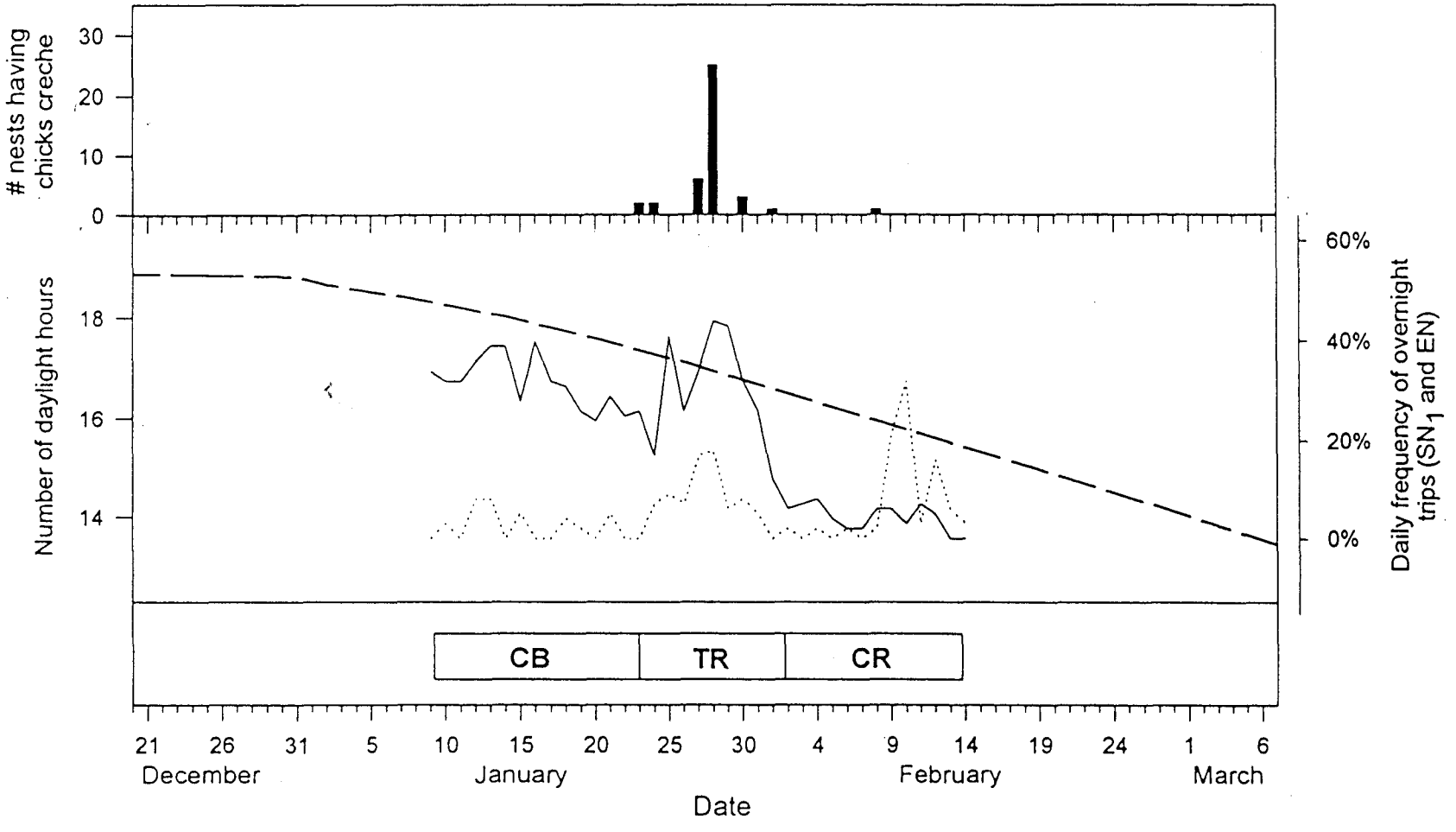

Figure 12. Daily frequency of standard (—) and extended overnight (·····) foraging trips during chick-brooding (CB), transition (TR), and creche (CR) periods relative to the progression of creching (upper panel) and the change in daylength (— —; lower panel) in 1993.

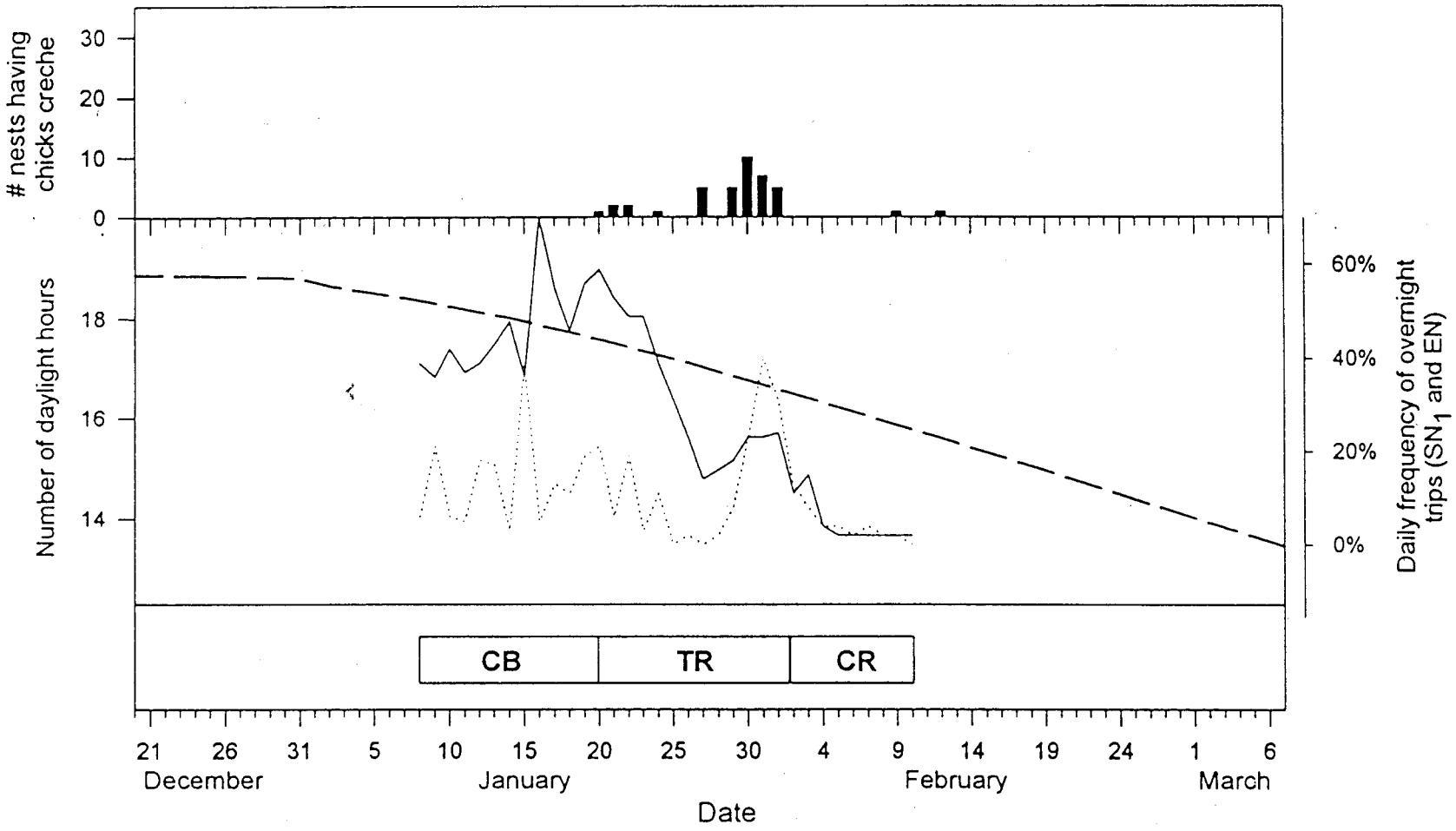

Figure 13. Daily frequency of standard (—) and extended overnight (·····) foraging trips during chick-brooding (CB), transition (TR), and creche (CR) periods relative to the progression of creching (upper panel) and the change in daylength (— —; lower panel) in 1994.

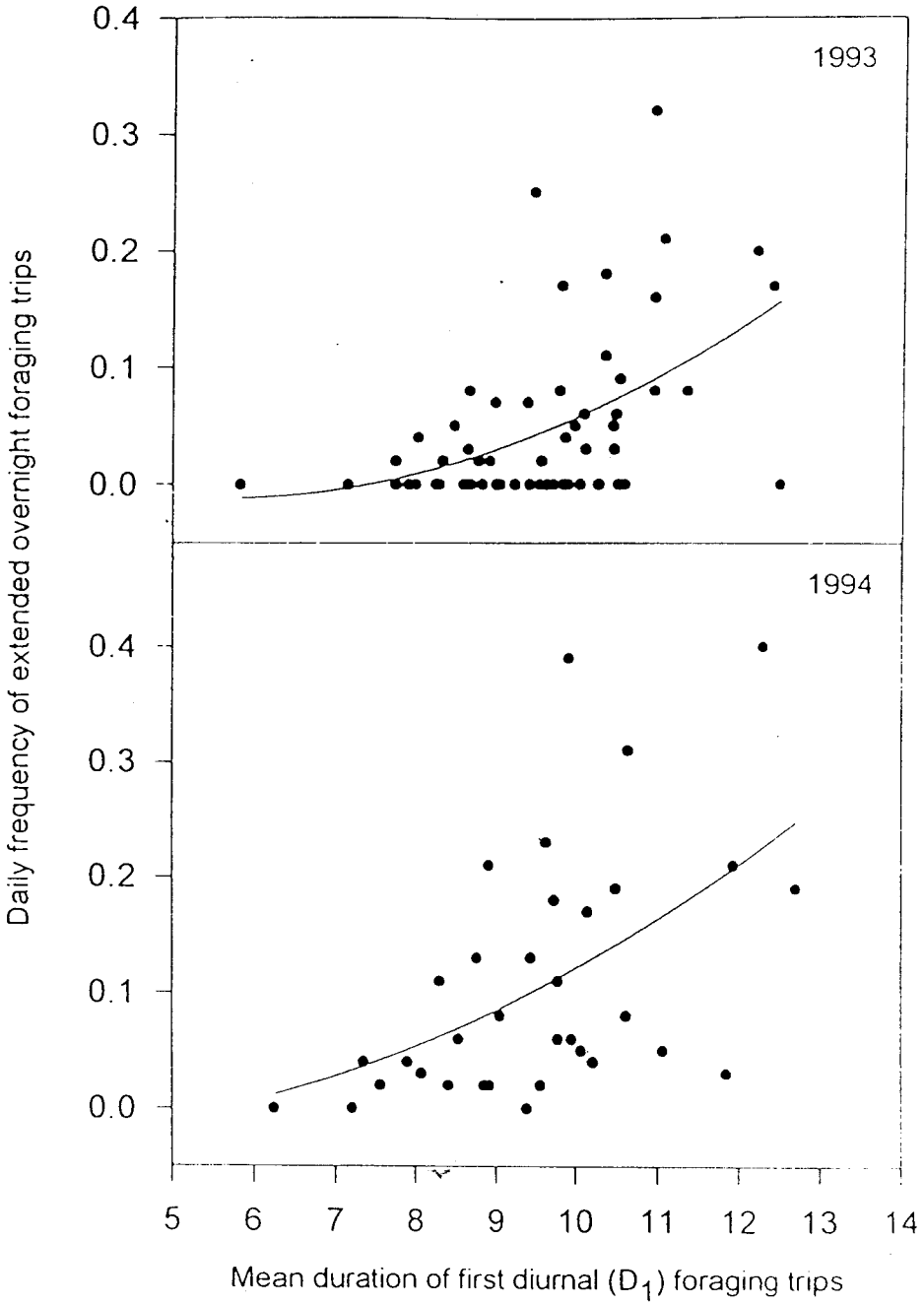

Figure 14. Relationship between daily frequency of extended overnight foraging trips and the daily mean duration of first diurnal foraging trips for 1993 ($y = -0.02x + 0.003x^2$, $r^2 = 0.66$) and 1994 ($y = -0.01x + 0.003x^2$, $r^2 = 0.64$). $P < 0.0001$ for both years.

sample from an overnight forager contained parts of fish flesh large enough to be recovered (286 grams), whereas in 1994, 15 samples contained between 2-347 grams of fish flesh. When fish occurred in the digested portion of the sample in 1994 it composed, on average, at least half of the identifiable prey (Table 5).

Whether foraging was conducted during the day or overnight had no significant effect on the mass of food brought ashore in either year (Two-way ANOVA, $F_{1,74} = 0.348$, $P = 0.55$). However, year did have an effect on food mass with the mean weight of samples in 1994 being heavier than in 1993 ($F_{1,74} = 18.93$, $P < 0.001$). The increased food mass in 1994 appeared to be the result of larger food loads in diurnal rather than overnight foragers but the trend was not quite significant (year-type of foraging trip interaction, $F_{1,74} = 3.67$, $P = 0.06$).

Table 5. Diet mass and composition and frequency of occurrence of fish in the diet of Chinstrap Penguins sampled after returning from diurnal (D) and overnight (ON) foraging trips. Intact and digested portions of the diet samples were examined separately in 1994 only.

					Mean % composition by weight								
					Intact [a]			Digested				No. of otoliths	
Year	Type of Forager	n	Mean Weight (g)(SD)	% intact (by wt.)	Krill	Fish	Squid	Krill	Fish	Squid	% occurrence of fish	Mean [b]	Range
1993	D	20	356 (146)	na	100	-	-	na	na	na	0	-	-
	ON	15	407 (148)	na	96	4 [c]	-	na	na	na	53	11	5-33
1994	D	20	595 (207)	62	100	t	-	98	t	-	5	6	na
	ON	20	499 (140)	60	96	3	-	42	43	< 1	85	45	1-180

[a] Because samples in 1993 were not separated into intact and digested portions, values for 1993 represent the entire sample.

[b] Only samples that had evidence of fish were included in the mean calculation. Two samples in 1993 and three samples in 1994, which had evidence of fish but no otoliths, were included in the mean calculation.

[c] Fish flesh was recovered from one sample containing 58% fish and 36% krill by weight.

t Trace: no flesh was recovered; only otoliths and eye lenses were found (weight < 1%)

CHAPTER IV

DISCUSSION

Critical Assumptions

Two important assumptions were made: 1) birds selected for instruments were a random sample of the population and 2) the transmitters did not influence the timing or duration of foraging trips taken by instrumented penguins. Conclusions drawn from the above results should consider possible errors in these assumptions. The potential biases introduced by using these assumptions are discussed below.

Sampling Regime

Because of concerns regarding disturbance of study birds and neighboring birds in the colony, it was not possible to select individuals randomly to receive transmitters. Due to the timing of deployments, selected birds may have been predisposed to exhibit one type of foraging behavior or another. However, deployments were conducted throughout the day, typically from 0800 h to 2000 h, thus including birds departing at a wide range of times. Results also showed that birds did not exhibit an obvious propensity to depart at a particular time of day throughout the season. In addition, the radio tags were deployed on birds from a large, but discrete, area within the colony to facilitate nest observations. The birds within this area are believed to reasonably represent the colony population as a

whole, although peripheral nests may have been slightly over-represented. A bias toward birds exhibiting a preference for departure time or a particular location within the colony is possible, but is likely to be small.

Potential Effects of Instrument Attachment

Streamlining is particularly important in animals that travel underwater as the fusiform shape of penguins and other marine vertebrates demonstrates (Bannasch et al. 1994). By attaching small devices to penguins, scientists have studied the movement and behavior of species that forage underwater substantial distances from land. These instruments, however, have the potential to influence the behavior they are designed to record, thus requiring an understanding of their effect before meaningful conclusions can be made (Wilson et al. 1989c, Wilson and Culik 1992, Culik et al. 1994).

Swimming speed in free-ranging penguins is influenced by the cross-sectional area of an attached device; birds swim more slowly with progressively larger instruments (Wilson et al.1986). For instance, Adélie penguins carrying an instrument about 1% of their cross-sectional area travel 3% slower than unencumbered birds (Wilson et al. 1989c). The effect of slower swimming on other foraging parameters, such as foraging trip duration, is not clear. Gales et al. (1990) and Croxall et al. (1988b) did not observe any effect on the time spent at sea for Little Blue (Eudyptula minor), Gentoo or Macaroni Penguins carrying devices that were less than 10% of the birds' cross-sectional area. However, Adélie penguins at Esperanza Bay make longer foraging trips carrying devices (1% cross-sectional area), although Wilson et al. (1989d) attribute this to anomalous

foraging trips taken by only 5 birds (25% of the birds with devices). In a study at Seal Island, Croll et al. (1991) reported that the foraging trip durations of Chinstrap Penguins carrying time-depth recorders (TDR; 5.3% of the bird's cross-sectional area) were not different from uninstrumented birds, but that trips taken by birds carrying a smaller transmitter (2.3%) were significantly longer than unencumbered controls. They attributed this inconsistency to the duration of transmitter attachment, which was two weeks longer than the TDR deployments, also citing the presence of the transmitter's antenna (absent on TDRs) as another possible source of disturbance. Croll et al. (1996), in a subsequent study using the same size instruments as in the present study (1% cross-sectional area), found no difference in the foraging trip durations between instrumented and non-instrumented Chinstrap Penguins at Seal Island. The difference in results between studies was attributed to the smaller frontal area of the transmitter and to applying less epoxy in its deployment.

By using these same streamlined transmitters attached as far back on the bird as possible, and by reducing the fouling of the contour feathers during attachment, I attempted to minimize the effect of instruments on the bird's foraging activity.

Arrivals and Departures at Night

Activity at night is rare in birds; those completing virtually all aspects of their life history between dawn and dusk represent less than one percent of the world's species (Martin 1990a). Periodic nocturnal activity in otherwise diurnal birds is much more common. How diurnal birds cope with nocturnal activity is not well known, but given the

restricted lifestyle imposed on strictly nocturnal birds (Martin 1986) it is surprising that mostly diurnal birds commonly undertake migrations during the night (Martin 1990a). While it is known that penguins are nocturnally active at sea during the night, as illustrated by diving activity (Croxall et al. 1988b for Macaroni Penguins; Kooyman et al. 1992 for King Penguins; Bengtson et al. 1993 for Chinstraps) and horizontal traveling (personal observation), it is apparent from this study that their capacity to transit to and from North Cove is limited by darkness. The lack of any activity at North Cove between 2300-0300 h suggests that light plays an important role in determining when birds leave or return to the island. It is significant that regardless of the behavioral context in which darkness occurs (e.g., active at sea or relatively inactive at the nest) the same reluctance to transit the island is observed. Because penguins are active on the water at night their reluctance to attempt a landing is presumably not governed strictly by a light-mediated endogenous clock, but possibly by an underlying behavioral adaptation to another environmental factor, such as predation or lack of prominent visual cues.

Leopard seals (Hydruga leptonyx) were observed capturing penguins at Seal Island (personal observation) and are commonly seen at other penguin breeding sites in the Antarctic (Penney and Lowry 1967). Significant leopard seal predation on breeding penguins may influence the number of trips taken by adults provisioning chicks (Chappell et al. 1993c). Chappell et al. (1993), who estimated that 11% of breeding Adélies at Palmer Station were eaten by leopard seals, calculated the risk of Adélie mortality by predation at 0.4% per trip, indicating a substantial risk when integrated over the entire period adults are making regular trips to sea. However, leopard seal predation on

breeding penguin populations elsewhere was deemed minimal (e.g., 2.4%, Müller-Schwarze 1984; 2.7%, Rogers and Bryden 1995).

The timing of leopard seal predation appears variable. There is no evidence of a diurnal rhythm in the predation on penguins by leopard seals at Cape Crozier (Lowry and Penny 1967). At Elephant Island, predation on penguins by leopard seals occurred only during the day with most seals hauling out at night (Conroy et al. 1975). In contrast, Müller-Schwarze (1971) noted that leopard seals were more likely to be in the water between 2000 h and 0400 h although a daily rhythm in predation activity was not reported. Reduced light might confer a visual advantage to leopard seals thus limiting the escape response in penguins, but there is no direct evidence that seals are better suited for vision at night. Even though information about predatory activities in leopard seals is sparse, it appears unlikely that an increased threat of predation could account for the virtual absence of transiting activity at night at North Cove.

A constraint on the navigational abilities of penguins may be a factor limiting nocturnal movements to and from the island. Two factors possibly involved in penguins returning to the colony after foraging offshore are: 1) navigation in an environment that provides few visual cues, and 2) negotiation of a complex and potentially hazardous coastline during a time when vision might be limiting. Adélie Penguins transported from their colonies to the Ross Ice Shelf invariably had more difficulty estimating the direction to the ice edge when the sun was obscured by clouds; birds released in clear skies showed little variability in the heading they chose while those released during heavy overcast were disoriented and selected departure headings at random (Emlen and Penney 1966). Other

studies have provided considerable evidence that visual cues are of primary importance in initiating and maintaining a course for birds migrating by day and night (Martin 1990b and references therein). Penguins are probably not exceptions and it is likely that the sun, and the features it illuminates, provides a basis for directional navigation during trips to sea. Further research on the movements of free-ranging penguins, during the day and at night, may reveal the factors most important in navigating a near featureless environment.

Reduced light may also impose a constraint to negotiating the complex and potentially hazardous coastline of Seal Island. In this case, visual acuity under reduced light might be a limiting factor. Spatial resolution in birds at low light levels is unknown (except for one species of owl; Fite 1973). On theoretical grounds, however, it is understood that the vertebrate eye is incapable of a high degree of spatial resolution at the lowest environmental light levels (Snyder et al. 1977). In a recent review, Martin (1990a) concluded that birds migrating at night, even in light conditions of maximum moonlight, were able to detect only the grossest details of their environment. The light gathering capacity and visual sensitivity of the penguin eye underwater fall within the range typically found in mammals and birds (Martin and Young 1984). The absence of departures and arrivals at North Cove at night, thus, could be the result of sensory constraints on the ability of penguins to both navigate to and from their foraging grounds and manage a safe transit of Seal Island's complex coastline.

Light-Dependent Foraging

Timing and Frequency of Foraging

The periodic and synchronized activity patterns recorded in the present study indicate that Chinstrap Penguins were using light as a predictable environmental cue for determining when to depart on a foraging trip and possibly when to terminate one. Specifically, the close correspondence between morning departures on diurnal trips and sunrise suggests that birds responded to rising light levels although certain inconsistencies suggest other factors might also be involved (see below). The greater degree of synchronization in morning departures relative to the arrivals in the evening indicates that light might trigger diurnal trip departures but play a lesser role in determining the end of a foraging trip. The synchrony of evening arrivals may roughly mirror the pattern of morning departures due to similarities in foraging times between individual birds. These results are consistent with Wilson et al. (1989a) who proposed light-dependent foraging by showing that Adélie Penguins are more likely to be at sea during periods of highest light intensity, especially a month after solstice when light levels at night fall below 30 lux.

Interestingly, birds completing overnight trips showed highly synchronized arrivals in the morning about 3 hours later than the first morning departures. Overnight foragers may be using rising light levels to either navigate back to the island or (and) to continue foraging prior to arriving at the island. Regardless, it is clear that birds were not simply waiting offshore for light levels to increase before attempting to land. Croll et al. (1993) speculated that an observed minimim in diving effort of Chinstrap Penguins just prior to

dawn and dusk occurs because birds change methods of prey detection based on solar light during the day to prey bioluminescence at night. They also suggested that krill (Euphausia superba), Chinstrap Penguins' primary prey, would become more difficult targets when aggregating and migrating downward at sunrise or dispersing and moving upward at sunset. The frequency of Chinstrap diving, as observed at Seal Island, begins to increase at sunrise (Bengtson et al. 1993, Croll et al. 1993). Whether this increasing effort occurs at the end of a overnight trip or the beginning of a diurnal trip is not known. If Chinstrap Penguins foraging at the outer limit of their foraging range (26 km; Bengtson et al. 1993) were to begin traveling back to North Cove at sunrise at a speed of 8.6 km · $hour^{-1}$ (Wilson et al. 1994), they would arrive at about 0630 h, a time that closely corresponds with morning arrivals during chick-brooding and transition when overnight trips are common. Thus, it appears that waiting until sunrise to initiate a journey back to the island could account for some of the delay in overnight foragers arriving back at the island. It is unlikely, however, that all penguins were foraging at their outer limit. Birds could be devoting time in the morning to feeding, possibly while maintaining a heading for the island or after positioning themselves closer to the island during the night.

The two modes of morning diurnal departures observed in 1993 suggest that the effects of light on foraging activity are mediated by other factors. These two modes occurred during chick-brooding and transition; the first mode coinciding with sunrise (as discussed above) and the second occurring about 3 hours later. The second mode of diurnal departures corresponded with the peak of arrivals for overnight foragers indicating this peak was mostly the consequence of birds waiting to be relieved by mates that had

been at sea overnight. If mated pairs mostly alternate diurnal and overnight trips while tending chicks, the frequency of these trips from a random sample of individuals within the colony would be about equal. In this case, a single mode of departures in the morning — corresponding to birds changing over after being relieved by an overnight forager — would result. If some pairs occasionally complete two diurnal trips (i.e., one each) within a day and forgo initiating a third trip (most likely a standard overnight trip), then the overall frequency of diurnal trips would increase and exceed that of overnight trips. Having these two patterns of pair-specific foraging (i.e., one diurnal-one overnight and one diurnal-one diurnal) occurring simultaneously within the colony would produce two modes of departures in the morning, resulting from some birds waiting for sunrise and others waiting for their mates. Thus, it is likely that the two modes of diurnal departures observed during chick-brooding and transition in 1993 were the result of at least two basic coordination routines within the same colony. This is further supported by the greater frequency in 1993 of birds taking single diurnal foraging trips compared to overnight trips, suggesting both adults at some nests were able to complete diurnal trips and not forage overnight.

The absence of this bimodal pattern of diurnal departures during the same periods in 1994 suggests that fewer pairs were foraging exclusively during the day and that the majority were alternating between diurnal and overnight foraging. A greater similarity in the frequency of overnight versus diurnal foraging in 1994 also indicates a more regular alternation between these foraging types. There is no evidence, however, that this regular alternation persists indefinitely. Individual foraging patterns show that most adults

exhibited diurnal and overnight foraging; very few birds specialized strictly on one type of trip during the study. The less typical patterns consisting of multiple trips per day and extended overnight trips might allow for a periodic switching of the foraging routine, such that birds feeding at night would eventually have an opportunity to feed during the day, and vice-versa. Hence, the need to coordinate activities with a mate to ensure successful chick rearing is an important constraint influencing the timing of foraging.

Comparisons with Other Sites

The foraging patterns of Chinstrap Penguins at Seal Island showed some important differences and similarities with other sites that experience a similar light regime. Chinstrap Penguins at Signy Island (60.4°S), during late-brooding, return from foraging trips throughout the daylight hours with only 35% arriving midday between 1200-1500 h (Lishman 1985b). Given a mean foraging trip duration of 39 hours (calculated from a feeding frequency of 0.62 trips per day; Lishman 1985b), it appears light levels may have less of an influence on the timing of arrivals, and possibly departures, in birds foraging longer than the daily light:dark cycle. The estimated maximum foraging range of Chinstraps at Signy Island, using trip duration, is 66-114 km offshore (Lishman 1985b). If this is accurate, the different foraging activity observed in Chinstrap Penguins at Seal Island — given their shorter foraging range (2-26 km) and trip durations — may indicate that light can influence gross activity patterns, but its effect may be mediated through potentially more important constraints such as distance to food resources.

Chinstrap Penguins brooding chicks in early January at Elephant Island exhibit a

bimodal pattern of arrivals and departures (Conroy et al. 1975); birds traveling to the sea show peaks in movement at 0400 h and 1030-1230 h with modes in number of birds arriving from the sea occurring at 0900-1100 h and 1830-2000 h. Observations of individual nests confirm that birds remaining in the colony with their mates overnight produce the pronounced peak in departures at 0400 h (Conroy et al. 1975). As at Seal Island, it appears that sunrise provides a cue for birds to depart. However, other aspects of the overall pattern at Elephant Island differ markedly from Seal Island. For instance, overnight foraging is apparently less common. The midday peak in activity coupled with a higher frequency of diurnal foraging trips — equivalent of 69% if one mate from each nest (n=8) were sampled as in the current study — suggests that adult pairs at Elephant Island more often complete two diurnal trips and less typically forage at night. Penguins at Seal Island may travel further and take longer trips to sea than Elephant Island birds, causing the typical daily foraging cycle (per pair) to be longer than the hours of available daylight. Longer foraging cycles coupled with a reluctance to transit the island at night may have forced penguins at Seal Island to adapt to a higher degree of nocturnality at sea. These differences between sites may also be the result of interannual variability in the distribution or abundance of prey. Chinstrap Penguins may intermittently utilize overnight foraging in response to a change in the local availability of prey. Shorter trips would allow both mates to forage within the hours of daylight, whereas longer trips would expand a pair's foraging cycle and necessitate overnight foraging.

Seasonal Changes in Foraging Patterns

While there is no direct evidence from this study that penguins are actually foraging at night, the large numbers of birds going to sea in the evening indicate that these trips are energetically beneficial to overnight foragers. A seasonal decline in the frequency of standard overnight foraging, however, suggests that foraging at night may be less advantageous once chicks begin to creche.

The decision by adults to leave chicks unattended in the colony has been suggested as a mechanism by which parents can spend more time foraging to keep up with the increasing demands of their growing chicks. The idea that the provisioning capacity of penguins influences the timing of creche is supported by evidence from Lishman et al. (1985a), who observed that creching in Chinstrap Penguins has a later onset than Adélies at the same site, citing a higher frequency of foraging trips and higher quality prey as a means for Chinstrap pairs to continue brooding longer than their congener. In addition, Chinstrap broods of two chicks creched more than 5 days earlier, on average, than single chick broods (Lishman 1985a). Indicators of the energetic costs of provisioning chicks also change after creching: adult mass and estimates of food remaining in the stomachs of adults after feeding chicks both reach a minimum just prior to creching in Adélie Penguins (Wilson et al. 1991, Culik 1994).

Without specific information on foraging patterns during creche, other studies estimating food delivery to penguin chicks have assumed that adults begin foraging simultaneously, thus doubling the frequency of chick feedings (Trivelpiece et al. 1987,

Culik 1994). This would, no doubt, be the case if each mate were to replace brooding shifts with foraging trips. Even though the frequency of birds in the present study initiating two trips in a day clearly increased after creching in both years, it did not double; the frequency of individual foraging trips per day increased only 12% and 44% in 1993 and 1994, respectively. Doubling the rate of food intake may not be adaptive for chick growth and survival; limitations on a chick's food assimilation rate might preclude the benefits of having twice the food delivered to it during a "simultaneous" visit from both parents.

The shift to diurnal foraging through the season, coupled with an increase in individual trip frequency, indicates that some penguins with creched chicks were increasing food intake by adding a diurnal foraging trip (or two) to their daily parental routine. The only modest increase in trip frequency, however, indicates that most pairs were not simply adding a diurnal trip to their current routine but rather were switching from overnight to diurnal foraging without a net increase in foraging effort. This indicates that, given the choice, Chinstrap Penguins preferred to feed during the day, at least later in the season. It is puzzling, however, that birds would stop utilizing overnight foraging, an apparently beneficial strategy, at a time when chick demands are highest (Trivelpiece et al. 1987, Culik 1994).

Given the evidence from the current study, and that from Lishman (1985a), it appears that the decision by Chinstraps at Seal Island to leave chicks unattended (i.e., creche) coincides with a decision to stop foraging overnight and that both result from limitations on food gathering. Two non-exclusive mechanisms which could account for

their decision to stop foraging overnight are: 1) adults are not able to adequately increase the rate of food delivery to growing chicks when alternating diurnal and overnight foraging, and 2) prey capture during overnight trips becomes more energetically costly later in the season, such that adults employing overnight foraging bring less food back to the colony as the season progresses. Longer and darker nights later in the season may further restrict the use of vision in penguins (Wilson et al. 1989a) making overnight feeding more costly. A seasonal shift in the distribution of prey, vertical or horizontal, may also make prey capture during late-season overnight trips more difficult. However, the precipitous nature of the decline in the frequency of standard overnight foraging in both seasons — occurring soon after adults began leaving chicks unattended — relative to more gradual seasonal changes in the daily light regime, suggests that increasing food demands by chicks may be the primary factor influencing the onset of creching. Despite this, a threshold response to declining prey availability, caused by seasonal changes in the light regime or other factors, cannot yet be ruled out. Irrespective of the exact mechanism, it appears that overnight foraging earlier in the season may simply be a necessary consequence of coordinating a foraging routine with one's mate even though diurnal foraging trips may have greater potential for prey capture. Release from this coordination constraint after creche may allow both mates to enhance prey capture by selecting the most efficient time of day to forage.

The preference for diurnal foraging may be based on a foraging inefficiency primarily during the darkest hours of overnight trips (Wilson et al. 1993). If so, the added flexibility afforded by creche might enable more diurnal foragers to exploit the early

morning (or evening) hours, when prey might be undergoing a behavioral shift that makes them more vulnerable to capture (Wilson et al. 1993), without having to remain at sea through the night. Chinstrap Penguins that did not have to wait for mates before departing in the morning began leaving the island during the hour of sunrise (except during creche in 1993). Studies recording the diving behavior of Antarctic Penguins carrying stomach sensors have shown a sharp increase in diving effort and prey capture when light levels were most dynamic (Wilson et al. 1993, Pütz and Bost 1994).

The greater incidence of overnight foraging in 1994, compared to 1993, indicates frequencies of types of trips fluctuated in response to environmental factors, one of which may be prey availability. Chinstrap Penguins may have evolved under selective pressure to exploit rapidly an unpredictable prey resource and bring food back to chicks at a higher rate when food is more available (i.e., complete foraging trips as quickly as possible). If this is the case, each mate would attempt to complete at least one diurnal foraging trip on a given day. Some parents would not be successful and the second attempt of the day would be an overnight trip. Of those parents that were successful, some birds would complete the second trip too late to allow their mate to initiate another trip before sunset (i.e., no overnight trips), whereas others would arrive early enough to provide the opportunity for an evening departure (i.e., increase in overnight trips). Because of the reluctance of birds to transit the island at night, overnight foraging may occur intermittently in concert with fluctuations in the amount of time each pair requires to complete two trips; overnight foraging would increase as a pair's foraging cycle approached minimal or maximal limits.

Determinants of Time Spent Foraging

The length of penguins' foraging trips is thought to reflect changes in food abundance in waters adjacent to breeding areas (Trivelpiece et al. 1987). It has been common to assume implicitly that penguins will spend less time at sea when prey is more abundant. Studies that demonstrate no correlation between the mass of food captured and the length of foraging trips suggest penguins do not return after a particular time interval, but rather after they have collected some minimum quantity of food (i.e., trip durations are variable; Croxall and Davis 1990). Miller and Davis (1993) suggested, however, that incubating Adélie Penguins are able to adjust their foraging budget at sea (i.e., resting less, foraging more) thus compensating for sub-optimal body condition or prey availability (i.e., trip durations are not variable). It is unlikely that parents provisioning chicks, however, have the same flexibility as those incubating and the need to return with food will have greater importance in determining the duration of their trips. Under these demands, the amount of time a bird is at sea is probably a function of foraging efficiency as has been suggested for Adélie Penguins (Miller and Davis 1993). This hypothesis is also supported by research on King Penguins in the Crozet Archipelago which extended their foraging trips and delivered less food to their chicks — causing reduced chick growth and increased mortality — during a time when availability of fish prey was declining in the region (Le Maho et al. 1993). Foraging trip duration in other seabirds has also shown a sensitivity to changes in prey abundance (Croxall et al. 1988a).

Consequence of Activity Patterns and Departure Time

Although evidence suggests that foraging may take longer when prey are less abundant, the relationship between prey availability and time spent foraging will be confounded when birds are restricted from initiating or terminating trips at certain times, as was the case at Seal Island during the night. There, the greater amount of time spent at sea by overnight foragers could be interpreted as evidence that nocturnal foraging is less successful than diurnal foraging. As indicated earlier, however, standard overnight trips might be the necessary result of coordinating with one's mate a daily feeding cycle that is longer than the period of available daylight. A bird that goes to sea in the late afternoon might collect enough food after being at sea for 8 hours (the length of an average diurnal trip), but may have to remain at sea until after sunrise because an arrival is restricted at night. As a result, the duration of overnight foraging trips may not be sensitive to changes in prey abundance and, therefore, may not directly reflect foraging success. The durations of diurnal trips, however, more likely reflect changes in foraging success, given that birds do not appear to be restricted from landing at any time during these trips.

That standard overnight foragers tended to synchronize their arrivals regardless of departure times suggests that, during the night when arrivals are restricted, these birds may have: 1) acquired, and were able to maintain, some minimal food load or (and) 2) realized an increasing risk of chick mortality with increasing time away from the nest. In either case, or if both occur, overnight foragers would be compelled to terminate trips at first opportunity in the morning. Those birds that acquire a minimal food load, but later

encounter difficulties foraging, may have to continue feeding in morning before provisioning chicks. If increasing light levels enhance foraging, birds may then quickly recoup energetic losses and (or) obtain a minimal food load causing most to arrive within a relatively narrow period. As overnight trips are prolonged, however, a shift in the motivation to terminate foraging — from acquiring a minimal food load to ensuring the survival of oneself and any offspring — may occur. As time at sea elapses, birds may have to weigh the benefits of 1) feeding oneself and 2) providing a sufficient meal for chicks, with the increasing risks of 1) chick starvation and 2) nest desertion by mates. That foraging trips are terminated at all suggests that adults have sufficiently replenished body fuels and have decided to provision chicks. Parents engaged in extended foraging trips may, thus, determine a period at sea that minimizes a negative effect on their own survival and, secondarily, that of their offspring.

Greater variability in the timing of morning arrivals, relative to departures, would suggest increased variability in foraging success among individuals, thus indicating a lessor importance for "nest" constraints in determining a bird's time at sea. Diurnal foraging trips, like overnight trips, are also shorter if taken later in the day, but show less dependence on departure time. This reinforces the idea that foraging success may play a greater role in determining length of diurnal trips.

Extended overnight trips are the equivalent of coupling diurnal and standard overnight trips. These, the longest trips, were typically initiated at a similar time as diurnal trips and terminated the following day amidst the mode of standard overnight arrivals. Even though standard overnight foragers may be influenced by a need to return to the

nest, the existence of extended overnight foraging trips indicates that birds can prolong foraging considerably, with most individuals doing so on more than one occasion. Interestingly, extended overnight trips also showed a stronger tendency than diurnal trips to be terminated at a particular time, although seemingly earlier in the morning than the shorter standard overnight trips. Birds that departed on extended overnight trips earlier, however, were the last the arrive the following morning. Two hypotheses that may explain why birds leaving the colony earlier arrive later are: 1) there is a foraging cost associated with earlier initiation of extended overnight trips such that additional foraging is required causing a delayed arrival, and 2) earlier departing birds are foraging further offshore and require more time, possibly in the morning, to travel back to the island. The positive relationship between the duration of first diurnal foraging trips and the frequency of extended overnight foraging in both years is consistent with the "foraging cost" hypothesis. If one accepts that the objective of foraging is to obtain some minimum amount of food to feed chicks and maintain body condition, then this relationship suggests that on days of reduced prey availability (i.e., longer diurnal trips), foraging success declines, and birds more frequently extend their trips to compensate. Ultimately, this would allow fewer birds to complete diurnal trips before sunset forcing them to remain at sea until the following morning. Hence, extended overnight trips may be functionally equivalent to "failed" diurnal trips rather than being a directed effort, as suggested earlier, to couple diurnal and overnight foraging trips allowing each member of a pair to forage at different times of the day. Extended overnight trips may, therefore, reflect those instances when a parent's own survival outweighs that of its chick(s).

Consequence of Variation in Available Light

Although the effects of variable light on vision in penguins have not been empirically tested, histological and ophthalmic studies suggest that penguins are well adapted to use vision in hunting their prey (Sivak 1976, Martin and Young 1984, Bowmaker and Martin 1985). Studies relating diving behavior and prey capture to time of day in penguins also emphasize the importance of vision (Wilson et al. 1989b, Wilson et al. 1993, Pütz and Bost 1994). It is perhaps not surprising, then, that in the present study, change in light intensity proved to be an important determinant of time spent foraging during the day, at least in 1993. Changes in light intensity are also believed to be the primary factors inducing diel vertical migration in marine zooplankton, including krill (see review in Ringelberg 1995). Therefore, while Chinstrap foraging may take longer on darker days due to a visual constraint, a light-triggered behavioral change in their prey may interact with this constraint making prey capture even more difficult.

Thus, at least two light-dependent factors may have been important in shaping a foraging strategy in penguins: 1) their ability to use vision during foraging, and 2) the behavior and distribution of their prey. If the influence of light on vision was the dominant evolutionary factor resulting in light-dependent foraging, it would be expected that variations in light would regulate a penguin's ability to use visual cues to locate prey. Wilson et al. (1989a) noted two physical processes that define a visual predator's ability to perceive prey: 1) there is a critical light intensity below which prey cannot be perceived, and 2) the ability to perceive prey increases with light intensity for values above the lower

critical intensity. Given the latter, it appears that the ability to perceive prey will vary with cloud cover and penguins will forage more successfully on sunny days, as the present study suggests.

However, when one considers the possibility that a light-mediated behavior of prey may also have played a role in the evolution of light-dependent foraging in penguins, the above argument is confounded. Krill swarms undergo vertical migrations in response to light (Ringelberg 1995, and references therein); Antarctic euphausiids rise to the surface and disperse at night and sink and form dense concentrations during the day (Kalinowski and Witek 1980, Everson 1982; Everson and Murphy 1987). Although there are exceptions to this pattern (Miller and Hampton 1989), where these migrations occur, they have been attributed to a life history trade-off between utilizing food in the surface layers and minimizing predation by visual hunters (Gliwicz 1986). It has been suggested, however, that diving predators more effectively exploit prey near the surface at night than at depth during the day (Lishman 1985b, Kooyman et al 1992). Even though Chinstrap Penguin diving appears to track the movement of vertically migrating krill — birds dive shallower at night than during the day (Bengtson et al. 1993; Croll et al. 1993) — dive depth may not be directly related to the vertical migration of prey. Instead, dive depth may primarily be a function of light availability (Wilson et al. 1993), which decreases exponentially with water depth. Wilson et al. (1993) and Pütz and Bost (1994) demonstrated that diving depth in King, Jackass, Adelie, Gentoo and Chinstrap Penguins, foraging in shallow waters at night, is not regulated by vertical migration in their prey because feeding at night rarely takes place. It was suggested, rather, that availability of

light regulates diving depth by influencing the utility of vision during prey capture (Wilson et a. 1993). Given that prey descend in response to increasing light — perhaps attempting to remain below the depth at which they are visible to predators — it is unclear how penguins would be relatively more successful foraging in brighter conditions, as suggested by the shorter trips taken on brighter days in the present study. That is, it seems that prey would simply migrate deeper on brighter days, rendering themselves no more vulnerable to penguins than on darker days.

Three hypothesis may explain this apparent contradiction. Firstly, the hours around twilight, especially sunrise, may be particularly vulnerable periods for prey (Wilson et al. 1993). At sunrise, those prey unable to migrate downward at a sufficient pace to stay below a penguin's visual threshold would become susceptible to predation. Cloudless mornings (or evenings) would produce more dynamic light changes possibly allowing penguins to more easily exploit those surface prey that could not descend quickly enough. Secondly, a photo-reactive response in zooplankton can be triggered in the presence of predators and inhibited by a shortage of food (Ringelberg 1995 and references therein). If krill swarms undergo vertical migrations in response to predators, then penguins might have the opportunity to exploit a prey patch for an initial period before individuals begin descending out of reach. If a shortage of food (i.e., phytoplankton) causes krill to disperse in the upper water column then, paradoxically, krill availability to penguins might be highest in years of lowest productivity. In either case, brighter days would provide more visual cues and increase the chances of a penguin finding an unexploited or "hungry" prey patch. Lastly, if the amount of time spent at sea is largely influenced by a bird's

ability to use visual cues to navigate, which would be enhanced by the sun, then one would expect darker conditions to hinder navigation and cause longer trips.

The effect of visual constraints on foraging can also be influenced by the sheer abundance of prey, independent of its behavior. When food is very abundant, a penguin might encounter prey at high rates whether daily light levels limited its visual range or not. If prey is very sparse, a penguin would less likely obtain a minimal food load even under good light conditions and probably be forced to return to the colony based on a need to feed chicks and relieve its mate. Thus, at the extremes of prey abundance, foraging trip length would be less dependent on light availability than at intermediate prey abundance. This might explain the lack of a negative correlation between diurnal trip duration and daily light levels in 1994

Hydroacoustic surveys around Seal Island during January indicate that regional krill abundance was more than ten times lower in 1994 than in 1993 (Hewitt and Demer 1994, Demer et al. 1994). Slightly longer diurnal foraging trip durations in 1994 suggest that more birds might have been closer to some maximal time for diurnal trips. The greater frequency of extended overnight trips during chick-brooding and transition in 1994 may also reflect a greater difficulty in capturing prey. Comparing trip durations during each of the breeding periods between years would more adequately address the question of whether more birds brooding chicks in 1994 might have had more difficult foraging, relative to 1993. Examining foraging trips during creche may not be useful because parents might not then be as compelled, by constraints at the nest, to return in as short a period of time as during chick-brooding.

Light-Dependent Differences in Diet

The efficacy of lavaging in obtaining complete stomach samples from penguins is now widely accepted (Wilson 1984, Gales 1987). Experimental feeding trials on Gentoo Penguins reveal that, up to 16 hours following ingestion of fish, all otoliths could still be recovered after three lavages (Gales 1987). After this time, only otoliths and fragments of fish were recovered; slightly less digested than those found in the present study, indicating that overnight foragers likely fed on fish early during their foraging trip. Free-ranging Jackass Penguins, after feeding on fish, required 10 to 12 hours of digestion before stomach flushing removed mostly bones and otoliths (Wilson 1985). Digestion occurs at different rates for different prey. Prawns (Penaeus indicus) fed to Gentoo Penguins took longer to digest when compared to fish and squid due in large part to their relatively indigestible exoskeleton (Jackson 1992). Jackson (1992) noted that the prawns, however, have thicker exoskeletons than the euphausiids naturally eaten by the birds and conclusions based on these results should be treated with caution. The effect of multi-prey meals on the relative digestibility of each component in penguins has not, to my knowledge, been examined.

Although krill may take slightly longer to digest than myctophid fish, the stark contrast between the upper layers of fresh krill and the almost completely digested fish recovered from the bottom of the stomachs of overnight foraging chinstrap penguins, coupled with the time taken to digest fish in other species, indicate that fish are primarily consumed during the first half of an overnight trip and krill during the later half. If this

stratification was the result of differential settling caused by varying density of prey (i.e., penguins captured fish as often as krill throughout the trip) then one would expect a freshly caught prey to be mixed with others of the same type that had been consumed earlier. That the layers of fresher krill and digested fish were consistently homogeneous in prey condition supports the hypothesis that the two prey types were captured at different times during the foraging trip. This evidence, in conjunction with the greater tendency of overnight foragers to feed on fish relative to diurnal foragers, suggests that fish are either targeted more often or are more available during the earlier part of overnight trips, or both. The almost equal representation of krill and fish in the digested portion of the samples in 1994, however, suggest that penguins feed on both prey types in the earlier portion of overnight trips. The layer of undigested krill, probably captured near the end of an overnight trip, supports the view that penguins intensify their foraging effort during the early morning hours possibly to utilize the rapidly increasing light levels by pursuing surface krill that may have temporarily become more visible. Stratification in the stomachs of diurnal foragers was less obvious, suggesting that diurnal foragers consumed prey at more regular intervals than overnight foragers.

Myctophid fish migrate to the surface at night to feed. A diel vertical migration from depths of 150-400 meters during the day to the upper 100 meters at night to feed has been demonstrated in two of the four myctophid species taken by penguins in this study (Electrona carlsbergi and Kreffrichthys anderssoni; Zasel'sliy et al. 1985, Perissinotto and McQuaid 1992). Zasel'sliy et al. (1985) discovered that fish tended to have more food in their stomachs at night; enhanced feeding by fish on krill occurred around sunset, for

about 6 hours, and just prior to sunrise, for about 2 hours. Thus, penguins at Seal Island may feed on fish and krill at dusk, when both vertebrate predators might have an advantage over their increasingly available prey, but feed exclusively on krill at dawn. Although as much as 15% of Chinstrap Penguin diving effort is expended at night (Bengtson et al. 1993), it appears — given the distinct prey-digestion strata in their stomachs and the reduced feeding success at lower light levels suggested in this study and others (Wilson et al. 1993, Pütz and Bost 1994) — that Chinstrap Penguins are not as proficient foraging at night as during the day.

It is perhaps perplexing, then, that diurnal and overnight foragers brought comparable quantities of food ashore in both years, especially when one considers that the time spent at sea during the night by overnight foragers may not be advantageous for feeding (Wilson et al. 1993, Pütz and Bost 1994). Overnight foragers may rely on an increased availability of fish and krill at dusk to balance the energetic requirements of remaining at sea through the night, even though feeding may be reduced. Birds may then anticipate being able to quickly acquire a minimum food load for chicks during the early morning hours, when krill may become more available. Almost two-thirds of the food brought ashore by overnight foragers was intact krill, likely captured during the few hours prior to terminating the trip.

Myctophid fish are considered meso-epipelagic, rarely occurring in the insular waters surrounding the shelf-slope region (Zasel'sliy et al. 1985; Perissinotto and McQuaid 1992). Not surprisingly, piscivorous predators such as the King Penguin (Adams and Klages 1987) can only meet their daily food requirement by traveling

extended distances (i.e., 28-120 km) to oceanic areas (Stahl et al. 1985, Kooyman et al. 1992). Consistent with this pattern, a recent study tracking the movement of Chinstrap Penguins to their foraging grounds north of Seal Island revealed that birds foraging diurnally remained within the shelf region, whereas overnight foragers traveled beyond the shelf to forage over the slope (Bengtson, unpublished data). Apparently, Chinstrap Penguins on overnight trips choose to forage in a different area, possibly one where prey are easier to capture during reduced light; the ventral light organs of myctophid fish may make them easier targets at night. Due to the offshore distribution of myctophids, however, their importance to foraging penguins may only be realized at the most distant point of their foraging excursion and, accordingly, evidence of fish may be defecated before arriving at the colony. This would tend to underestimate the relative contribution of fish in the diet of birds that might be traveling further offshore (e.g., Chinstraps at Signy Island).

Previous studies indicate that Chinstrap Penguins feed primarily on krill (Volkman et al. 1980, Lishman 1985b Trivelpiece et al. 1990) with a few noteworthy exceptions (Croxall and Furse 1980; Jablonski 1985). Chinstrap Penguins in the Elephant Island Group had, by weight, 96% Euphausia superba in their stomachs with only 7% of the birds showing evidence of fish (Croxall and Furse 1980). However, at two sites, 40% of the birds had evidence of fish but otoliths were not enumerated and time of foraging was not noted, making the importance of fish difficult to assess in that study. If relatively few birds from Elephant Island forage at night, as suggested by Conroy et al. (1975), the population may rely less on fish than the birds at Seal Island. During six breeding seasons

at King George Island, Chinstrap Penguins relied heavily on krill in all years except one (Trivelpiece et al. 1990); in 1980/81, sampling conducted by Jablonski (1985) indicated that 65% of the diet was composed of fish with the remainder being krill (17%) and amphipods (5%). A strong peak in chick feeding at about 0700 h suggests that birds were taking overnight trips (Jablonski 1985) but because the time of diet sampling was not reported, comparisons between years and sites are not possible.

These findings, and those of the present study, indicate that the importance of fish can vary between years. The significantly greater incidence of fish in the diet of overnight foragers in 1994 coincides with a depression in regional krill abundance (Demer et al. 1994). Penguins may target fish more often when krill is less available or fish may be more vulnerable when their own food source is limiting (e.g., as in krill). Relating diet composition in penguins to results of simultaneous sampling of prey, as well as information about whether penguins change foraging areas in concert with changes in prey availability, would be required to test this hypothesis.

Similar to Meyer et al. (1996), analyses in this study showed that food loads were larger in 1994, however, this seemed to be the result of greater foraging success in diurnal rather than overnight foragers. The apparent contradiction between reduced krill abundance and increased food loads in penguins during the 1994 season has been attributed to the inadequacies of large-scale krill surveys in reflecting what was actually available to penguins (Meyer et al. 1996). They suggested high-density patches of krill within 50 km of Seal Island in 1994 allowed penguins to maintain high rates of food delivery to chicks even though krill was less available in a regional sense. If this is the

case, diurnal foragers may have better success at locating more isolated patches of krill than birds feeding by night.

To my knowledge, no studies examining foraging in Chinstrap Penguins (or any penguin) have considered the daily timing of foraging as a potential variable influencing what prey is eaten. The present study confirmed that krill is important to breeding Chinstrap Penguins. By taking account of light-dependent foraging patterns, however, this study also presents evidence that fish are a persistent and significant feature in the diet of Chinstrap Penguins at Seal Island, suggesting a greater role for fish in their energy budget than previously thought. In conjunction with information about foraging areas in Chinstrap Penguins, this study presents evidence that fish may be specifically targeted by Chinstrap Penguins during overnight trips. Thus, information on when and where foraging takes place is necessary to clearly interpret prey importance and make comparisons between sites more informative.

Summary of Conclusions

Chinstrap Penguins taking daily trips to sea to provision chicks at Seal Island foraged either during the day, overnight, or, less frequently, for an extended period through the day and subsequent night. Birds rarely initiated two trips in a day while brooding chicks, but, with increasing frequency, took two consecutive diurnal trips after chicks began to creche. Individual penguins did not specialize on any one type of foraging trip. Overnight foragers spent significantly more time at sea than diurnal foragers, but a reluctance to transit the island at night may have caused overnight foragers to extend their

foraging trips independent of any change in prey availability. Departure time had a variable effect on the duration of foraging trips depending on the type of trip; overnight foragers had a stronger tendency to terminate trips at a particular time (in the morning) rather than after a particular interval of time, than did diurnal foragers. This suggests the need to relieve a mate and bring food back to the nest takes on greater importance when a bird is at sea for an extended period of time through the night. This also indicates that durations of diurnal foraging trips are likely to be more sensitive, than durations of overnight trips, to changes in prey availability. That a shift to less diurnal and more overnight foraging occurred between 1993 and 1994 indicates that the frequency of types of trips varies in response to changes in the environment.

The penguins' synchronized and predictable daily foraging rhythm is largely a response to daily changes in light levels. Birds used increasing light levels in the morning to initiate diurnal foraging; penguins rarely left the island before sunrise. Diurnal foragers arrived in the early evening, providing mates the opportunity to begin foraging before declining light levels precluded a departure from the island. Birds terminated overnight foraging in the morning about three hours after sunrise, suggesting that other factors, such as navigational constraints or increased prey availability at dawn, may influence the arrivals of overnight foragers. Consequently, the morning departures of adults whose mates had been foraging overnight were not as closely coupled with sunrise. Darkness precluded virtually all departures from and arrivals to the island. The role of light in triggering morning departures was enhanced later in the season when parents were not strictly coordinating with each other.

The sudden shift to diurnal foraging as chicks began to creche in both seasons indicates that mates are better able to meet the increasing food demands of their chicks by foraging exclusively during the day. Utilizing nighttime and crepuscular periods for foraging may be obligatory during chick-brooding when a penguin's opportunity to forage is dictated by the arrival of its mate. Overnight foraging was rarely exhibited after chicks were left unattended and parents began foraging more independently of one another. Diurnal foraging may take precedence because nocturnal prey capture could be difficult for visually-orienting penguins, especially later in the season when nights are longer and darker, but the sudden change to diurnal foraging suggests adults were not able to balance food acquisition with increased chick demands, necessitating a shift to a more efficient mode of foraging. The incidence of extended trips, in which birds coupled diurnal and overnight trips, showed no seasonal trend. Rather, these trips were more frequent on days in which diurnal trips were longer. These extended trips appear to represent diurnal foraging trips in which arrivals were mistimed or not attempted due to unsuccessful foraging. That diurnal trips were longer on darker days in one season indicates that relatively small fluctuations in light, which can occur during daylight hours, influence the availability of prey. This coupled with the apparent preference for diurnal foraging further supports the hypothesis that overnight foraging is not as beneficial as diurnal foraging.

That only overnight foragers feed on fish also indicates that light influences the availability of prey, perhaps by a penguin visual constraint or light-mediated shift in the behavior of prey. The offshore distribution of myctophid fish suggests that overnight foragers may be exploiting a different feeding habitat than diurnal foragers; one that may

offset additional energetic costs that nocturnal foraging may incur. The greater incidence of fish in the diet of overnight foragers in 1994 indicates the occurrence of myctophids can vary widely between years. This study demonstrates that timing of foraging influences the diet of Chinstrap Penguins at Seal Island indicating that studies elsewhere should sample birds at different times of the day to rigorously assess diet.

Further research on penguin foraging behavior will become increasingly fruitful as biologists learn to distinguish aspects of feeding that are coupled with physical processes from those that are genuine responses to changing biological components of a penguin's environment, such as prey abundance. Future ecological studies could greatly benefit from controlled experiments examining the response in captive penguins to variable feeding conditions and detailed observations of penguins feeding in the wild. A greater knowledge of the sensory abilities penguins have evolved to inhabit marine environments will undoubtedly lead to a better understanding of their ecology.

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